

Bangor University

DOCTOR OF PHILOSOPHY

Depth zonation patterns of benthic communities and reef production framework on contemporary coral reefs

Sannassy Pilly, Jyodee

Award date: 2023

Awarding institution: Bangor University

Link to publication

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- · Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
 You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Depth zonation patterns of benthic communities and reef framework production on contemporary coral reefs



Thesis submitted by Sivajyodee Sannassy Pilly, BSc (Hons) MSc October 2023

For the degree of Doctor in Philosophy School of Ocean Sciences, Bangor University Wales, UK

"Nature is not fragile . . . what is fragile are the ecosystem services on which humans depend" (Levin 1999)

Aya Balakrishna, Goindama, Ramsamy, Savedhi & Nades

Declaration and Consent

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy. This thesis was completed under the supervision of Professor John Turner and Dr Ronan Roche, who provided intellectual guidance, financial support, and critical reviews of manuscripts . During this research, I was responsible for the project concept and design, data collection, analysis and interpretation and drafting and revision of manuscripts. Data for Chapter 2–3 was also collected by Prof John Turner and Dr Ronan Roche. Dr Ronan Roche and Dr Laura Richardson contributed to benthic community analysis (image analysis) that was used in Chapter 2–3. Data collection for Chapter 4 was assisted by Dr Ronan Roche, Dr Laura Richardson, Dr Andrew Mogg and Katherine Dawson. Chapter 4 was completed with contributions from co-authors: Dr Ines Lange and Professor Chris Perry, who assisted with conceptual advice on study design and revision of manuscript.

Acknowledgements

I would first like to thank my supervisors John Turner and Ronan Roche for this wonderful opportunity to work at the School of Ocean Sciences and in the Chagos Archipelago. Thank you both for your guidance, support, and encouragement in particular in my most challenging times. Merci beaucoup and indefinitely for the impromptu meetings, insightful discussions, prompt feedback on data analysis and write-up, and deciphering what I am often trying to say with my bilingual brain!

I would also like to acknowledge the Bertarelli Foundation for funding my doctoral studies and the wider group from the Bertarelli Programme in Marine Science with whom I had the opportunity to work during field trips and conferences. Huge thanks to the Grampian Frontier and Pacific Marlin crew for their assistance and patience for having us on board during fieldwork, and REV Ocean for the once in a lifetime opportunity of a 500 m deep dive.

To Laura Richardson, thank you for invaluable time spent id'ing benthic images, and support with data analysis and reviewing manuscripts. Special thanks to Lucy Southworth for assistance with frame grabbing, Johnathan Ball with R code design, Lucille Chapuis with Matlab code design. Huge thanks to the Bangor University Reef Systems research group for providing the space to discuss ideas and presenting my work. Thank you to the Nautilus crew (current and past) and staff in SOS for your friendship and amazing times.

To Tidana, Tigoulou and Lekip Pilly in Mauritius – thank you so much for supporting and encouraging me from the other side of the world, this would not have been possible without you! To Lesley and John Ball – I am forever grateful for your kindness and encouragement. To Sam Hollick – diolch yn fawr fy nghariad, for your support and for cheering me always.

Abstract

Increasingly frequent and severe climate-driven warming events are one of the main drivers of change on tropical coral reefs. However, the degree to which disturbance events affect ecological communities is not uniform across space and varies across environmental gradients. Similarly, the extent to which the structure and function of benthic communities within shallow water habitats (<30 m) vary and respond to recurring thermal stress across different depth gradients remains unclear. Most assessments of bleaching and degradation are carried out at depths <10 m, limiting our understanding of the depth variability in the changes in benthic assemblages and vertical zonation in response dynamics. This disproportionate focus of coral reef studies at shallow depths further limits our understanding of the zonation in vital geo-ecological functioning such as primary framework production on rapidly changing coral reefs under current climate trends. Importantly, increasing evidence of bleaching and mortality reported within both shallow (<30 m) and mesophotic reef zones (30–150 m) currently requires the review of the Deep Reef Refugia Hypothesis, which suggests that coral reefs at depth can escape the impacts of thermal stress events.

Using benthic community data from the Chagos Archipelago, a relatively remote reef system in the Central Indian Ocean, this thesis aims to provide an understanding of the depth zonation patterns of recent past climate change impacts on contemporary shallow coral reefs. In the absence of direct anthropogenic impacts, the uninhabited atolls of the Chagos Archipelago can be used as an ecological baseline to measure the extent of future thermal stress events on dynamics and geo-ecological functioning of shallow coral reef benthic communities across depths. Importantly, isolated reefs provide the opportunity to understand the natural ecological limits of coral reef ecosystems, which can be used to inform important management and conservation strategies to preserve coral reefs. Whilst there is natural variation in the ecology of benthic communities with depth, it is expected that the change in community assemblages and ecological functions following thermal anomalies will cause additional variation across depth zones, with larger changes at shallower depths due to more dynamic environmental conditions and greater compositional variability across reefs. By assessing community assemblages across multiple depth gradients (5–25m) this thesis: (1) examined the variation in depth zonation in benthic communities within and among different reef sites; (2) assessed the response of benthic communities across depth to recurring warming events; and (3) analysed the variation in coral carbonate production across depth gradients.

Depth zonation in benthic forereef slope communities prior to the back-to-back bleaching events in 2015–2017 was assessed and compared in shallow (5–10 m) and deep (20–25 m) benthic community assemblages among and within atolls (**Chapter 2**). Whilst within-atoll comparisons revealed distinct differences between shallow and deep forereef slope communities, the variation in both major functional groups and hard coral assemblages varied with depth among atolls. These results suggest that the spatial variation in depth zonation of benthic communities may be driven by biophysical processes that concomitantly vary across depths and atolls.

The response of different benthic lifeforms was then measured across a 5–25 m depth gradient following successive marine heatwaves in 2015–2017 (**Chapter 3**). There was an overall decline in hard and soft coral cover and an increase in crustose coralline algae, sponge, and reef pavement. By assessing the effects of initial and repeated thermal stress, variable benthic community response to elevated seawater temperatures was observed across depths: the loss in hard coral assemblage was associated with initial thermal stress compared to soft coral cover loss that was better predicted by repeated thermal stress, with greater changes in benthic group cover at shallow (5–15 m) than at deeper (15–25 m) reef zones following successive warming events. Despite reduced changes in benthic group cover with increasing depth, the findings in this thesis revealed that repeated bleaching impacted benthic communities at depths up to 25 m.

Finally, the zonation in primary framework production was examined using a dataset 6-7 years following the 2015–2017 warming events, through an assessment of coral carbonate production rates across shallow (10m) and moderate (17.5 m) forereefs, and the importance of coral morphotypes and colony size classes on the spatial variation in carbonate production rates was evaluated (**Chapter 4**). Results revealed consistently higher coral cover and coral carbonate production on shallow reefs than at moderate reefs, which significantly varied among atolls. Coral morphotypes that significantly contributed to production processes on shallow reefs included small, medium, and large colonies of branching *Acropora* and massive *Porites* as well as other large branching corals. In contrast, higher occurrence of encrusting and foliose corals of all size classes largely contributed to carbonate production rates at moderate depths. Comparing two census-based approaches, the *ReefBudget* method provided a more realistic estimate of carbonate production rates compared to *CoralNet*, which employs an areanormalised scaling technique and Monte-Carlo simulation, which predicts the probability of coral carbonate production rates based on an estimated range of taxa-specific coral colony sizes

and calcification rates., Slower recovery of branching and tabular corals at shallow depths at one out of four atolls, indicate the likely impacts of recurrent bleaching during the 2015–2017 warming events on the depth-homogenisation of coral community and carbonate production.

This thesis develops understanding of depth zonation patterns in benthic community changes and geo-ecological functions within contemporary shallow reef systems. It indicates heterogenous vertical zonation of benthic communities and highlight the potential ecological consequences of shifts in benthic community assemblages and primary framework production across depths. This research highlights the on-going threats of climate change on coral reef benthic communities and underline the importance of measuring how the impacts of disturbances vary across depth gradients. The overall results from this thesis have important implications for understanding long-term dynamics of vertical structuring of shallow coral reef benthic communities and ecosystem function, especially in the face of the Deep Reef Refugia Hypothesis debate and under the predicted increase in climate-induced warming events.

Table of Contents

Declara	tion and Consentiv
Stateme	ent of contribution of othersv
Acknow	vledgementsvi
Abstrac	tvii
Table of	f Contentsx
List of l	Figures xiii
List of 7	Tablesxv
Chapter	1: General Introduction
1.1	Changing community ecology1
1.2	Contemporary coral reef benthic communities and ecosystem resilience1
1.3	Changing geo-ecological functioning of contemporary reefs
1.4	Depth zonation on contemporary reefs4
1.5	Aims and thesis outline
Chapter	2: Atoll-dependent variation in depth zonation of benthic communities on remote
reefs	
Abstr	ract7
2.1	Introduction
2.2	Methods10
2.2	.1 Study sites
2.2	.2 Benthic composition
2.2	.3 Data analysis
2.3	Results
2.3	.1 Variation in major functional groups14
2.3	.2 Variation in hard coral assemblage
2.4	Discussion

Chapte	er 3: I	Depth variation in benthic community response to repeated thermal str	ress on
remote	e reefs		
Abs	tract .		
3.1	Int	roduction	29
3.2	Ma	terials and Methods	
3.	2.1	Study Sites	
3.	2.2	Data collection and benthic community assessment	
3.	2.3	Estimating change in benthic groups following 2015–2017 bleaching	ig events33
3.	2.4	Exposure to repeated thermal stress	
3.	2.5	Data Analysis	35
3.3	Re	sults	
3.	3.1	Variation in benthic community composition after 2014–2017 mari	ne
he	eatwar	ves	
3.	3.2	Depth-dependent temporal change in benthic composition	
3.	3.3	Effects of thermal stress on change in benthic communities across of	lepth zones
3.4	Di	scussion	
V	ariatio	on in ecological response to initial and repeated thermal stress	53
a)	Ch	ange in hard coral cover following bleaching events	53
b)) Ch	ange in other benthic groups following bleaching events	54
B	enthic	community reorganisation following thermal stress	55
D	epth z	conation on coral reefs in warming climate	
Chapte	er 4: E	Effects of depth on coral carbonate production on remote reefs	
Abs	tract .		58
4.1	Int	roduction	59
4.2	Me	ethod	61
4.	2.1	Study Sites	61
4.	2.2	Benthic community composition	

4.2.3	Coral carbonate production
4.2.4	Coral colony size structure
4.2.5	Statistical analyses
4.3 Res	sults
4.3.1	Benthic community composition
4.3.2	Coral cover and carbonate production71
4.3.3	Contribution of coral morphotypes to total coral carbonate production75
Chapter 5: C	eneral Discussion
5.1 Ke	v findings
5.2 Imp	plications for present and future coral reefs
5.3 Fut	ure directions research and recommendations
5.4 Cor	nclusion
References	
Appendix A	- Supplementary materials for Chapter 2: Atoll-dependent depth variation in
depth zonati	on of benthic communities on remote reefs91
Appendix B	- Supplementary materials for Chapter 3: Depth variation in benthic community
response to 1	epeated thermal stress on remote reefs
Appendix C	- Supplementary materials for Chapter 4: Effects of depth on coral carbonate
production of	n remote reefs

Figure 2.1: Map of Chagos Archipelago showing sampled sites
Figure 2.2: Non-metric dimensional scaling (nMDS) of major functional groups showing
clustering by depths15
Figure 2.3: Variation in major functional groups (generalised linear mixed effects models)
between depth (5–10 m (grey) and 20–25 m (black)) a16
Figure 2.4: Non-metric dimensional scaling (nMDS) of coral genera assemblage, showing
clustering by depths
Figure 2.5: Proportional cover (%) of indicator coral genera across atolls:20
Figure 3.1: Map of sampled sites (red points) around surveyed atolls (in bold) in the Chagos
Archipelago
Figure 3.2: Peaks of thermal stress indicated by monthly maximum Degree Heating Week
(maxDHW) during the 2015–2017 recurring warming events
Figure 3.3: Non-metric multi-dimensional scaling plots (nMDS) of benthic groups from 16
sites in the Chagos Archipelago, showing clustering of communities in 2013/14 (pre)
and 2018/19 (post) following the 2015–2017 marine heatwaves across depth zones (39)
Figure 3.4: Predicted mean change in benthic groups cover following the 2015–2017 marine
heatwaves across depth zones: 5–10 m, 10–15 m, 15–20 m, 20–25 m40
Figure 3.5 : Posterior distributions of the standardised effects of initial and repeated thermal
stress on the change in hard coral cover following the 2015–2017 marine heatwaves43
Figure 3.6 : Posterior distributions of the standardised effects of initial and repeated thermal
stress on the change in soft coral cover following the 2015–2017 marine heatwaves45
Figure 3.7 : Posterior distributions of the standardised effects of initial and repeated thermal
stress on the change in crustose coralline algae (CCA) cover following the 2015-2017
marine heatwaves47
Figure 3.8 : Posterior distributions of the standardised effects of initial and repeated thermal
stress on the change in reef pavement following the 2015–2017 marine heatwaves49
Figure 3.9 : Posterior distributions of the standardised effects of initial and repeated thermal
stress on the change in sponge cover following the 2015–2017 marine heatwaves51
Figure 4.1: Map of sampled sites (red points) around surveyed atolls (in bold) in the Chagos
Archipelago62

Figure 4.2: Calibration and measurement of coral colony-size using 50 x 50 cm quadrat in J-
Microvision64
Figure 4.3: Non-metric multi-dimensional scaling (nMDS) plots of a) benthic groups and b)
hard coral assemblage from 16 sites in the Chagos Archipelago69
Figure 4.4: a) Predicted coral cover between shallow (10 m) and moderate (17.5 m) depths
and b) posterior distributions of standardised effects of depth on variation in coral cover.
Figure 4.5: a) Predicted coral carbonate production between shallow (10 m) and moderate
(17.5 m) reefs and b) posterior distributions of standardised effects of depth on variation
in coral carbonate production73
Figure 4.6: Regression between transect level coral carbonate production rates (Coral G
measured in kg CaCO ₃ m ⁻² yr ⁻¹) from <i>CoralNet</i> against rates from <i>ReefBudget</i> 74
Figure 4.7: Contribution of coral morphotypes to coral carbonate production (coral G)
between shallow (10 m) and moderate (17.5 m) reefs between CoralNet and ReefBudget.

Table 2.1: Within-atoll variation in major functional groups using One-way permutational
analysis of variance (PERMANOVA) between depth (5-10m vs 20-25m)14
Table 2.2: Within-atoll variation in major functional groups between depth (5–10m vs 20–
25m) using generalised linear mixed effect models (GLMM) at: Egmont (EG), Great
Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA)17
Table 2.3: Within-atoll variation in the hard coral assemblage between depth using one-way
permutational analysis of variance (PERMANOVA) at : Egmont (EG), Great Chagos
Bank (GCB), Peros Banhos (PB) and Salomon (SA) in the Chagos Archipelago in 2013
Table 2.4: Within-atoll variation in common indicator coral genera using generalised linear
mixed effect models (GLMM) at: Egmont (EG), Great Chagos Bank (GCB), Peros
Banhos (PB) and Salomon (SA)
Table 2.5: Indicator coral genera at atolls- Egmont (EG), Great Chagos Bank (GCB), Peros
Banhos (PB) and Salomon (SA) at shallow (5-10m) and deep (20-25m) sites22
Table 3.1: Variation in benthic community before and after the 2015–2017 marine heatwaves
using permutational analysis of variance (PERMANOVA) and dispersions tests a)
across depth zones and b) among atolls within-depth zones
Table 4.1: Variation in benthic community using permutational analysis of variance
(PERMANOVA) and dispersions tests between shallow and moderate reefs across and
within atolls70
Table 4.2: Variation in hard coral assemblage using permutational analysis of variance
(PERMANOVA) and dispersions tests between shallow and moderate reefs across and
within atolls71
Table 4.3: Predicted coral cover (mean \pm SE) between shallow (10 m) and moderate (17.5 m)
reefs with average standardised effects of depth on variation in coral cover across atolls:.
Table 4.4: Predicted coral carbonate budget (mean \pm SE) between shallow (10 m) and
moderate (17.5 m) reefs with average standardised effects of depth on variation in coral
carbonate budget across atolls

1.1 Changing community ecology

Assessing community configurations and their response to environmental changes is an important part of ecology. By explaining how communities vary across space and time, the study of community dynamics provides useful insights into the environmental and ecological niche of communities (Agrawal et al. 2007). Ecological systems across biomes are highly dynamic and show high spatiotemporal heterogeneity (Blowes et al. 2019). Ecological drivers that vary across natural gradients dictate the spatial and temporal variability in communities, and arise from complex interactions between organisms and their environment, constraining the diversity, abundance, and composition of species and therefore the communities we observe (Gentili et al. 2013; Gove et al. 2015; Roik et al. 2018).

However, over the past few decades, global warming and pervasive local stressors have markedly altered natural ecosystems across biomes (Blowes et al. 2019). Rising global temperatures, biogeochemical change, pollution, overharvesting, land-use modification, habitat destruction and their combinations systematically modify ecological processes, leading to increasingly homogenised community structure across ecosystems (McElwain 2018; Kennedy et al. 2019; Williams et al. 2019). Following a disturbance event, communities shift to assemblages better adapted to altered ecological conditions (Malhi et al. 2014; Beger 2021). The patterns observed in altered communities are intrinsically linked to non-random modifications in population life histories driven by continuously changing environmental conditions (Werner and Prior 2013; Darling and Côté 2018). However, the chronic nature of disturbance events in the Anthropocene is increasingly leading to less predictable changes in composition, diversity, and function across space and time (Havrdová et al. 2023; Ford et al. 2023).

1.2 Contemporary coral reef benthic communities and ecosystem resilience

On coral reefs, the combination of global-scale climate stressors and local-scale anthropogenic impacts have caused widespread declines in benthic communities across multiple spatial and temporal scales (Williams et al. 2019). In recent decades, there have been increasing reports of altered species composition, regime shifted reefs and structural framework loss due to land-use change, water quality deterioration (Edinger et al. 1998; Brown et al. 2017; Carlson et al. 2019),

overfishing (Roberts 1995; MacNeil et al. 2015; Shantz et al. 2020), disease outbreaks (Weil 2004; Lamb et al. 2018; Vega Thurber et al. 2020), increased cyclones and storm intensity (Harmelin-Vivien 1994; Hernández-Delgado et al. 2014; Cheal et al. 2017) and increasingly frequent and more severe warming events (Hughes et al. 2018a; Eakin 2022). Significant shifts in community patterns and distribution can be observed, mainly due to the loss of foundation coral species, which consequently alter the interactions between coral reef benthic groups (Dornelas et al. 2014; Reverter et al. 2022). Replaced by fast-growing opportunistic benthic taxa, alternative non-coral dominated states are often characterised by an increase in macroalgae, turf, sponge, soft corals, zoanthids, cyanobacteria, ascidians, anemones and/or corallimorpharians (Wee et al. 2017; Bell et al. 2018; Reverter et al. 2022; Tebbett et al. 2023).

Resilience is an ecosystem's or population's ability to resist, absorb and recover from environmental changes without changing into another stable yet compromised state (Hughes et al. 2010). Whilst coral benthic communities can recover to pre-disturbance levels, often after long recovery periods and in the absence of direct anthropogenic impact (Sheppard et al. 2013b; Gouezo et al. 2019; Sheppard et al. 2020), communities also undergo succession and return to hard coral dominated assemblages, but characterised by altered coral community composition (Adjeroud et al. 2018; Darling et al. 2019; González-Barrios et al. 2021). Climate-induced bleaching events are one of the main causes of degradation in coral reef benthic communities (Hughes et al. 2017b; Lough et al. 2018; Oliver et al. 2018a). Unlike short-term acute stressors (e.g. cyclones) from which coral reefs often recover, chronic back-to-back bleaching events can compromise the ability of coral reef communities to reassemblages (Connell et al. 1997; Adjeroud et al. 2009; Gouezo et al. 2019).

Including disturbance history, non-random community changes vary as a function of community plasticity and modifications in environmental and ecological conditions (Torda et al. 2017; Darling and Côté 2018). As different taxa show different susceptibilities to thermal stress, novel coral community configurations tend to display reduced coral diversity and an increase in small, weedy and stress tolerant coral species (Darling et al. 2013; Toth et al. 2019). In the absence of disturbances, it can take between 7 to 13 years for coral reefs to reassemble and recover to pre-disturbance levels (Adjeroud et al. 2009; Sheppard et al. 2013b, 2020; Gouezo et al. 2019). However, as severe warming events become more frequent and intense, smaller recovery windows impede coral community recovery (Osborne et al. 2017), with direct knock-on effects on the reassembly of benthic communities (Hughes et al. 2017b, 2018a). The

predicted increase in large-scale disturbance events such as severe warming events (van Hooidonk et al. 2016) raise concerns about the functioning and resilience of shallow coral reefs to recurrent thermal stress.

1.3 Changing geo-ecological functioning of contemporary reefs

The rate at which benthic communities are changing has important implications on the key geo-ecological functioning of coral reefs (Perry and Alvarez-Filip 2019; Williams and Graham 2019). These functions include the maintenance of reef framework, sediment generation that sustains beaches and shorelines (Kench and Cowell 2000; Laing et al. 2020), coastal protection against wave energy (Beck et al. 2018), habitat provision for reef fish communities and other associated organisms (Graham and Nash 2013; Ferrari et al. 2018), all of which underpin the ecosystem goods and services that coral reefs provide (Kennedy et al. 2013; Woodhead et al. 2019).

One of the core ecological functions of coral reefs is carbonate accretion (Brandl et al. 2019). A reef's carbonate budget is quantified as the sum of gross carbonate production (mainly by hard corals and calcareous encrusters such as crustose coralline algae) and removal processes (including dissolution, erosion by bio-eroding taxa such as parrotfish, sponge and worms, and physical import/export of sedimentary materials) (Chave et al. 1972; Perry et al. 2008). Driven by the community composition, reef carbonate budgets naturally show significant variability among and within reef habitats (Lange et al. 2020; Brown et al. 2021). However, as habitatbuilding corals decline following severe bleaching and are competitively replaced by alternate benthic taxa, changes in carbonate producing processes alter reef framework development and maintenance, leaving structurally flatter and homogenised coral reefs (Magel et al. 2019; Elliott et al. 2018) with low positive to net negative budget states (Molina-Hernández et al. 2020). It is estimated that degraded reefs with low carbonate budgets and decreased net accretion rates will be more prone to submergence due to sea-level rise under current climate trends, posing significant threat to coastal communities and reef islands (Perry et al. 2018). Serving as a proxy of reef functional state and health (Perry et al. 2008), temporal and spatial variation in reef carbonate budgets across different reef habitats can provide important insights into the effects of disturbance driven changes on contemporary reefs (Perry and Morgan 2017a; Manzello et al. 2018).

1.4 Depth zonation on contemporary reefs

Despite being naturally heterogenous, the distribution and organisation of benthic organisms on shallow coral reefs (<30 m) exhibit specific depth zonation patterns (Sheppard 1982; Done 1983; Kahng and Kelley 2007; Williams et al. 2013; Edmunds and Leichter 2016). The vertical structuring of benthic communities is driven by biophysical factors such as light, temperature, salinity, wave energy and primary production, that naturally vary across water depth gradients (Kleypas et al. 1999; Kahng et al. 2019; Radice et al. 2019a). For instance, shallow coral species occurring at high light and high wave energy environments typically show dominance of branching and corymbose morphologies capable of tolerating large temperature fluctuations and shedding suspended materials (Marcelino et al. 2013; Gove et al. 2015; Guest et al. 2016). Comparatively, deeper reef zones are characterised by low-relief building corals with encrusting and foliose morphologies adapted to efficiently capture lower light levels with increasing depth (Kahng and Kelley 2007; Lesser et al. 2010; DiPerna et al. 2018). Similarly, an increase in mixotrophy and heterotrophy can be observed in deeper communities (Houlbrèque and Ferrier-Pagès 2009; Williams et al. 2018), as oceanographic processes such as internal waves and current-driven and deep-water upwelling import nutrient subsidies onto shallow reefs (Aston et al. 2019; Radice et al. 2019). As benthic communities morphophysiologically adapt to variable biophysical forcings across depth, it can be expected that benthic communities to predictably vary across depth gradients.

Depth zonation research has been key in elucidating some of the ecological and physical factors that drive the variation in coral reef benthic communities (Done 1983; Sheppard 1980a; Bridge et al. 2011a; Kahng and Kelley 2007; Williams et al. 2018). By studying the depth range over which generalists and specialists occur, studies have explained the range and boundary limits of species distribution (Keith et al. 2015; Roberts et al. 2019) and clarified the overlap that exists between communities at different depth zones (Laverick et al. 2018; Rocha et al. 2018; Roberts et al. 2019). Importantly, depth zonation of benthic communities has informed the understanding of complex dynamics such as regime shifts and divergent ecological trajectories within shallow reefs (Graham et al. 2015; Gouezo et al. 2019).

However, the consistency of how coral reef benthic communities and the functions they provide vary spatially across depths remains unclear. The degree to which recurring bleaching events affect benthic communities is not uniform across space and varies across environmental gradients (Blowes et al. 2019; Bridge et al. 2014a; Adjeroud et al. 2018; Baird et al. 2018). The disproportionate focus of coral reef studies on shallower depth ranges (<10 m) limits our

understanding of the variation in benthic community response to increasing thermal stress and contemporary community dynamics (Graham et al. 2015; Osborne et al. 2017; Gouezo et al. 2019) across the extent of shallow tropical reefs (0 – 30 m). Similarly, whilst carbonate budgets are increasingly being used to assess contemporary geo-ecological functioning of rapidly changing shallow reef systems, the variability in carbonate producing processes within reef zones >10 m deep remains unclear. As 97% of carbonate budget estimates originate from \leq 10 m deep reefs, the paucity of data at greater depths limits our understanding of how geo-ecological functions changes spatially across depths (Lange et al. 2020).

Contrary to classic depth-dependent patterns observed decades ago prior to contemporary changes in coral reef communities (Goreau 1959; Sheppard 1982; Done 1983), recent studies show context-specific vertical zonation following disturbance events, indicating that depth zonation patterns vary as a function of community dynamics at a locality and are becoming less predictable following recurrent disturbance events (Edmunds and Leichter 2016; Richardson et al. 2023). Moreover, many have hypothesised that deeper coral reef communities can act as a potential refuge, where surviving communities can repopulate impacted shallow reefs (Glynn 1996; Bridge et al. 2011; Semmler et al. 2017; Laverick et al. 2018). However, in contrast to the depth refugia theory, increasing evidence of coral bleaching and mortality across wider depth gradients in both shallow (2-27 m) and mesophotic depths (>30 m) shows that coral communities at depth are not immune to increasing anthropogenic impacts affecting shallow reefs (Bridge et al. 2013; Smith et al. 2016; Rocha et al. 2018; Diaz et al. 2023). Large scale thermal stress events are predicted to occur annually in the Anthropocene (van Hooidonk et al. 2016). How benthic community distribution and patterns vary spatially is key to our understanding of their response to rapidly changing environmental conditions and to predict how coral reef communities might respond in the face of future disturbance events (Hughes et al. 2019; Williams and Graham 2019).

1.5 Aims and thesis outline

This thesis aims to bridge current knowledge gaps in our understanding of the vertical variation in benthic community composition and the geo-ecological functioning of coral communities in the context of systemic changes on shallow coral reefs. Using benthic community data from the Chagos Archipelago, a relatively isolated reef system in the Central Indian Ocean, this research examines climate change impacts on the structure and functioning of shallow coral reefs across depths ranging from 5–25 m deep. Specifically, through three data chapters, this thesis addressed the following questions:

- 1. Does depth zonation in benthic communities vary within and among contemporary reef systems?
- 2. How do benthic communities across depth respond to recurring warming events?
- 3. How does important reef function such as carbonate production vary across depth?

Chapter 2 compares coral reef benthic communities between shallow (5-10 m) and deep (20 -25 m) sites at two spatial scales: among and within four atolls and assesses the variation in depth zonation in benthic forereef slope communities prior to the back-to-back bleaching events in 2014–2017. **Chapter 3** assesses depth-dependent changes in benthic communities following the 2015–2017 successive marine heatwaves and examines the trajectory of community changes by analysing effects of initial and repeated thermal stress across a 5–25 m depth gradient. **Chapter 4** examines the vertical zonation in primary framework production of reef budget processes following 6-7 years of recovery after the 2015–2017 back-to-back bleaching events. This study assesses the coral carbonate production rates at shallow (10 m) and moderate (17.5 m) depths across four atolls and evaluates the importance of coral morphotypes and colony size classes on the spatial variation in carbonate production rates.

Chapter 2: Atoll-dependent variation in depth zonation of benthic communities on remote reefs

Abstract

The distribution and organisation of benthic organisms on tropical reefs are typically heterogenous yet display distinct zonation patterns across depth gradients. However, there are few datasets which inform our understanding of how depth zonation in benthic community composition varies spatially among and within different reef systems. Here, we assess the depth zonation in benthic forereef slope communities in the Central Indian Ocean, prior to the back-to-back bleaching events in 2014-2017. We compare benthic communities between shallow (5–10 m) and deep (20–25 m) sites, at two spatial scales: among and within 4 atolls. Our analyses showed the variation in both major functional groups and hard coral assemblages between depth varied among atolls, and within-atoll comparisons revealed distinct differences between shallow and deep forereef slope communities. Indicator taxa analyses characterising the hard coral community between depths revealed a higher number of coral genera characteristic of the deep forereef slopes (10) than of the shallow forereef slopes (6). Only two coral genera consistently associated with both depths across all atolls, and these were Acropora and Porites. Our results reveal spatial variation in depth zonation of benthic communities, potentially driven by biophysical processes varying across depths and atolls and provide a baseline to understand and measure the impacts of future global climate change on benthic communities across depths.

Published:

Sannassy Pilly S et al, 2022. Atoll dependent variation in depth zonation of benthic communities on remote reefs, Marine Environmental Research.

DOI: 10.1016/j.marenvres.2021.105520.

2.1 Introduction

One of the main goals in ecology is to understand how communities occupy space. Biotic (González et al. 2017; Des Roches et al. 2018), abiotic (McGill et al. 2006; Agrawal et al. 2007), and stochastic processes (Hubbell 2005) that are responsible for the organisation of ecological communities, interact and create natural environmental gradients in biophysical resources (Leibold and McPeek 2006; Vellend 2010; Brandl et al. 2019). These naturally occurring gradients combine to limit the distribution, abundance, and diversity of communities (Holt 2003; Peischl et al. 2015). Similar natural variations occur across water depth gradients on tropical reef systems, where biophysical conditions known to influence the physiology of reef organisms co-vary, such as light availability (Brakel 1979; Hoegh-Guldberg and Jones 1999; Cooper et al. 2007), temperature, salinity (Kleypas et al. 1999), and wave and current regimes (Lowe and Falter 2015; Radice et al. 2019). Coral reef species develop different traits to survive within variations of these parameters across depths (Kneitel and Chase 2004; McGill et al. 2006; Darling et al. 2012). As a result, distinct and predictable ecological zonation patterns in coral reef ecosystems can be observed across depths (Sheppard 1982; Done 1983; Roberts et al. 2015; Karisa et al. 2020).

Different zones on shallow coral reef systems are usually defined by the occurrence of one or more dominant organisms that occupy a certain depth in a location (Goreau 1959; Sheppard 1982; Done 1983). For instance, zonation patterns in shallow forereef slope communities are described as being predictably dominated by structurally robust species. Coral species exposed to high light regimes and large temperature fluctuations on shallow areas of the reef slope have adapted morpho-physiologically to this dynamic environment (Titlyanov and Titlyanova 2002; Iglesias-Prieto et al. 2004; Marcelino et al. 2013; Guest et al. 2016). Often prone to high exposure to wave and surge energy (Done 1983), some shallow water species are adapted to thrive in areas where frequent sediment resuspension occurs, forming robust morphologies which can resist high water flow and physical forces (Todd 2008; Duckworth et al. 2017). In contrast, deeper forereefs which are more sheltered from surface wave exposure and receive lower irradiance due to light attenuation with depth (Done 1983; Rex et al. 1995), are characterised by coral communities that frequently adopt encrusting and foliose growth forms to increase light capture efficiency (Titlyanov and Titlyanova 2002; DiPerna et al. 2018). There is also an increase in mixotrophic and heterotrophic traits in marine organisms, such as hard corals, soft corals and sponges to offset limited light availability in deeper reef zones (Fabricius and Klumpp 1995; Fabricius and De'ath 2008; Houlbrèque and Ferrier-Pagès 2009).

Our understanding of the consistency of how coral reef benthic communities vary spatially across depths remains unclear (Edmunds and Leichter 2016; Roberts et al. 2019). This may be due to the complex interactive effects of biophysical processes that drive ecological community structure, which vary across multiple spatial and temporal scales (Hatcher et al. 1987; Magurran 2004; Leibold and McPeek 2006; Vellend 2010; Brandl et al. 2019), resulting in highly heterogenous coral reef communities (Edmunds and Bruno 1996; Huntington and Lirman 2012; Obura 2012; Dalton and Roff 2013; McClanahan et al. 2014; Ford et al. 2020). In addition, much of our current understanding of depth zonation patterns on reefs is based on observations made decades ago (Goreau 1959; Done 1982; Sheppard 1982; Done 1983), prior to subsequent climate change impacts that have altered coral reef communities (Dubinsky and Stambler 2010; Williams et al. 2019).

Coral reefs around the world are increasingly vulnerable to more intense and frequent climatedriven disturbances (Anthony 2016; Hughes et al. 2017a, 2018b; Perry and Alvarez-Filip 2019). However, the extent at which coral reefs are affected by anthropogenic stressors is not uniform across space and varies across depths (Bongaerts et al. 2010; Bridge et al. 2014a; Baird et al. 2018). Examining depth zonation of benthic communities in the context of systemic disturbance has provided important insights into complex dynamics such as diverging ecological trajectories and regime shifts, but these studies have been generally limited to shallow (3–10 m) depth ranges (Graham et al. 2015; Gouezo et al. 2019). This focus on shallow depth ranges has limited our understanding of how benthic community composition change across different depths within contemporary shallow tropical reefs (<30 m) (Bridge et al. 2014b; Edmunds and Leichter 2016).

Here we examined depth zonation in benthic community composition at two spatial scales (among and within atolls) in the Chagos Archipelago, a relatively isolated reef system in the Central Indian Ocean, prior to pan-tropical bleaching events in 2014–2017 (Eakin et al. 2019) and post 1998 bleaching (Sheppard 1999a). Isolated reefs can be used an ecological reference point (Sandin et al. 2008; Smith et al. 2008; Williams et al. 2013; Heenan et al. 2017; Head et al. 2019a) and examining benthic communities, prior to the back-to-back bleaching event in 2014–2017, establishes a baseline to measure the extent of further climate change impacts and how these vary across depths. Specifically, we compare benthic composition among and within four atolls, between two depth ranges: 5–10 m and 20–25 m on the forereef slopes. With our current knowledge of depth dependent zonation on coral reefs (Done 1982; Sheppard 1982;

Done 1983), we expected to find zonation across depth in benthic community composition that was consistent amongst atolls.

2.2 Methods

2.2.1 Study sites

The Chagos Archipelago is located in the centre of the Indian Ocean, at the remote southern end of the Laccadives-Maldives-Chagos ridge, ~500 km from south of Maldives (Sheppard 1999b). The archipelago is comprised of 5 atolls, 52 islands, and constitutes 9400 km² of submerged shallow reefs (<40 m depth) (Dumbraveanu and Sheppard 1999; Sheppard et al. 2013a). The archipelago has been largely uninhabited since the early 1970s (Sheppard, 1999), with the exception of Diego Garcia (DG), the southern-most atoll that hosts a US naval facility, where strict environmental regulations are enforced, prohibiting all commercial fishing and extractive activities at sea (Purkis et al. 2008). In this study, a total of 26 sites; including 13 at 5–10m depth (hereafter 'shallow' reefs) and 13 at 20–25m depth (hereafter 'deep' reefs), were surveyed on forereef slopes across 4 atolls: Peros Banhos (PB), Salomon (SA) (northern atolls), Great Chagos Bank (GCB) and Egmont (EG) (southern atolls) (Figure 2.1, Appendix A Table S1).



Figure 2.1: Map of Chagos Archipelago showing sampled sites (red points) around surveyed atolls (in bold) – northern atolls: Peros Banhos (PB), Salomon (SA) and southern atolls Great Chagos Bank (GCB) and Egmont (EG) - see Appendix A Table S1 for list of sites and coordinates.

2.2.2 Benthic composition

At each site, benthic composition was quantified from 30 digital photo-quadrats taken in February and March 2013 (total across all sites, n = 780). Digital photo-quadrats were randomly extracted as still images from 10 min continuous video-swims at both 5–10 m and 20–25 m depths. The housing was equipped with two spotlights and two red laser pointers set at 10 cm apart to provide a consistent scale-measurement of the benthos and to adjust for lower-light levels at greater depth to facilitate benthic image analysis. The camera was maintained approximately 0.5 m above the substrate and at a 45° angle to capture benthic organisms under overhangs and canopies (Goatley and Bellwood 2011).

Each video was converted into an image sequence (25 frames per sec; in Pinnacle Studio, v22.2.0). To ensure that images selected for analysis did not contain the same section of the

forereef, frames were randomly selected, but separated by a minimum of 80–100 frames (Matlab, R2018a.Ink). Benthic image analysis was carried out by SSP, RR, and LR using Coral Point Count with excel extensions (CPCe) (Kohler and Gill 2006). To account for any variation in observer bias in identification of benthic composition, the frames were equally divided among observers and analysed (10 images each per person per site). Proportional cover of benthic categories was quantified by identifying substrate and benthic organisms under fifteen randomly allocated points on each image, with one point assigned within a 3 x 5 grid cell stratification (Suchley 2014).

Substrate type and benthic organisms were categorised as: hard coral (identified to genus), soft coral (identified to family), non-scleractinian coral (*Millepora*, *Heliopora* and *Distichopora*), sponge, crustose coralline algae (CCA), macroalgae, turf algae, bare substrate with algal film (hereafter bare substrate), sand, rubble (< 10 cm maximum length), dead coral, bleached coral, diseased coral, 'other live' and unknown. 'Other live' included all sessile invertebrates such as bryozoans, tunicates, bivalves, giant clams, corallimorphs, anemones and zoanthids. Soft corals were identified and grouped within the four most common families occurring in the archipelago – Alcyoniidae, Xeniidae, Nepthtiidae and Nidaliidae (Schleyer and Benayahu 2010), or other soft coral. Where image quality limited identification of hard corals to genus level or morphology (approximately 0.1-0.5%), corals were classified as 'other'. The classification of benthic categories for this study was based on NOAA Coral Reef Information System (2014), Dennis et al, (2017a) and the CATAMI classification system (Althaus et al. 2015).

2.2.3 Data analysis

To assess whether benthic composition varied across depths, and if depth zonation varied among atolls, benthic community composition was first visualised at two levels: 1) proportional cover of major functional groups (hard coral, soft coral, sponge, CCA, macroalgae, turf algae, bare substrate with algal film, sand and rubble, non-scleractinian coral, bleached coral, dead coral, diseased coral, 'other live'), and 2) proportional cover of hard coral assemblages, identified to genera. Benthic composition was visualised across: a) depth, and b) atoll, using non-metric Multidimensional Scaling (nMDS: vegan package; Oksanen et al., 2012), based on a Bray-Curtis dissimilarity matrix of square root transformed data. A scree plot was used to evaluate ordination stress and a Shepard stress plot to confirm correlation between the original dissimilarity matrix and the distances on the final nMDS plot. The nMDS was computed on 3

dimensions (k = 3) with a stress value ≤ 0.1 . The envfit function (vegan package) was used to fit vectors of major functional groups and coral genera, to their respective nMDS ordinations.

To assess differences in benthic composition across depth and atolls, we performed two-way nested permutational multivariate analyses of variance (PERMANOVA; Anderson 2017) on: 1) major functional groups, and 2) coral genera, as a function of the interaction between atolls (4 atolls; fixed factors) and depths (2 depths; fixed factors), with sites (random factors) nested in atoll (9999 permutations; adonis2 function: vegan package). Average within-group dispersion was examined using a multivariate homogeneity test (betadisper: vegan package). Where a significant interaction between depth and atoll was found, we tested for variation in 1) major functional groups, and 2) coral genera across depths at each individual atoll using one-way nested PERMANOVAs. Data were square-root transformed and analysed using Type III sum of squares to accommodate an unbalanced design, in both one-way and two-way PERMANOVA.

Indicator taxa analyses were used to determine the association between coral genera and the depth ranges at which they occur. Coral genera that significantly associated with shallow and deep reefs across each atoll, were used to infer on the biotic and abiotic state of the environment that prevail at the different depth ranges (Cáceres and Legendre 2009). Prior to analysis, the proportional cover matrix of the coral genera assemblage was converted into presence/absence data. Coral genera characteristic of shallow and deep reefs were identified using a p-value threshold of <0.05 (9999 permutations, indicators: indicspecies package; Cáceres 2020).

Generalised linear mixed-effects models (GLMMs) with a binomial distribution and logit-link function were used to model major functional groups within each atoll, treating depth as a fixed effect and sites as a random effect (glmer: lme4 package, Bates et al. 2015). GLMMs were also performed on coral genera that consistently characterised the hard coral assemblage across both depths and all atolls. When major functional groups or coral genera cover had a high number of zeros and did not fit the standard binomial distribution (> 55% of the data consisted of zero values), a zero-inflated generalised linear mixed-effect models with a beta distribution was fitted (depth as a fixed factor and sites as a random factor; glmmtmb: glmmTMB package; Brooks et al. 2017). All analyses were performed using R 3.5.1 (R Development Core Team 3.5.1, 2018).

2.3 Results

2.3.1 Variation in major functional groups

Within-atoll analyses revealed significant variation in major functional groups between shallow and deep reefs across all four atolls (PERMANOVA, all: p = 0.001, Table 2.1, Appendix A-Figure S1). There was also an interactive effect of depth and atoll (PERMANOVA, Pseudo F_{3, 779} = 13.54, p = 0.001) and dispersion (Appendix A Table S2) on benthic composition, indicating the variation in major functional groups between depth varied among atolls; notably at EG and PB (Figure 2.4, Table 2.1, Appendix A Table S2)

Table 2.1: Within-atoll variation in major functional groups using One-way permutational analysis of variance (PERMANOVA) between depth (5–10m vs 20–25m) at: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) df- degree of freedom

Atoll	PseudoF-ratio	df	p-value
EG	46.844	1, 179	< 0.001
GCB	5.156	1, 179	< 0.001
PB	48.943	1, 119	< 0.001
SA	28.208	1, 229	< 0.001



Figure 2.2: Non-metric dimensional scaling (nMDS) of major functional groups showing clustering by depths, based on Bray-Curtis dissimilarities of square-root transformed data in a total of 26 sites in the Chagos Archipelago. Coloured ellipses represent dispersion of depth centroids at 95% confidence limit – blue: shallow sites (5-10 m) and red: deep site (20-25 m). Symbols represent surveyed atolls _ Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Vectors represent major functional groups distribution to the patterns on the ordination plot. Red labels in (a) indicate a significant contribution and black labels indicate a non-significant contribution.

A decreasing hard coral, bare substrate and dead coral cover was observed with increasing depth compared to CCA, macroalgae, sand and rubble and sponge cover which increased on the deep forereef slopes at EG (Figure 2.3, Table 2.3). At PB, hard coral and dead coral cover also decreased with depth compared to sand and rubble, sponge, soft coral, and turf algae cover which increased on the deep forereef slopes (Figure 2.3, Table 2.3). At GCB, only dead coral cover varied significantly with depth (Figure 2.3, Table 2.3). At SA, macroalgae and 'other live' cover increased significantly with depth while dead coral showed a significant decrease with increasing depth (Figure 2.3, Table 2.3).



Figure 2.3: Variation in major functional groups (generalised linear mixed effects models) between depth (5–10 m (grey) and 20–25 m (black)) across atolls - Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) in Chagos Archipelago 2013. * represent p <0.05 (see Appendix A Table S4)

Table 2.2: Within-atoll variation in major functional groups between depth (5-10m vs 20-25m) using generalised linear mixed effect models (GLMM) at: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). BS – Bare substrate, CCA – crustose coralline algae, HC – hard coral, MA – macroalgae, DC- dead coral, OL – other live, SR – sand and rubble, SP – sponge, T – turf, BL – bleached coral, UK – unknown, NS – non-scleractinian coral. In bold are significant p-values. df- degrees of freedom

Atoll														210
		BS	CCA	HC	MA	DC	OL	SR	SC	SP	Т	BL	UK	NS
EG	Coeff	0.628	-1.464	1.052	-2.189	1.742	-1.269	-1.158	-0.393	-1.294	0.078	-	0.032	-
	SE	0.210	0.287	0.322	0.607	0.397	1.009	0.521	0.865	0.340	0.215		0.461	
	p-value	0.003*	< 0.001	0.001	< 0.001	< 0.001	0.209	0.026	0.650	< 0.001	0.717		0.946	
	Coeff	0.466	-0.573	-0.356	-0.456	0.5418	-1.122	-0.733	-1.021	-0.105	0.321	0.321	0.740	-
GCB	SE	0.384	0.867	0.461	1.204	0.189	0.978	0.418	0.991	0.819	0.499	0.499	1.153	
	p-value	0.225	0.509	0.440	0.705	0.004	0.251	0.079	0.303	0.898	0.520	0.193	0.521	
	Coeff	0.732	0.260	2.165	-1.399	2.864	-0.359	-2.096	-0.944	-1.698	-1.622		0.088	
PB	SE	1.092	0.320	0.244	1.035	0.657	0.624	0.710	0.293	0.543	0.519	-	0.167	-
	p-value	0.503	0.416	< 0.001	0.176	< 0.001	0.566*	0.003	0.001	0.002	0.002		0.589*	
SA	Coeff	0.642	-0.490	0.398	-2.119	1.628	-2.966	-1.292	-0.698	-0.624	-0.395		0.150	-0.791
	SE	0.392	0.252	0.418	0.516	0.357	0.948	0.840	0.650	0.509	0.303	-	0.335	1.983
	p-value	0.101	0.052	0.341	< 0.001	< 0.001	0.002	0.124	0.283	0.221	0.192		0.654	0.690

'-' could not compare as groups did not occur at both depths, '*' zero inflated model using GLMMTMB

2.3.2 Variation in hard coral assemblage

Thirty-seven coral genera were recorded across all sites, with a higher number of coral genera were recorded at deep reefs (34) than shallow reefs (23). SA contained the highest coral genera richness (29), followed by GCB (22 genera), PB (20 genera) and EG (16 genera). Within-atoll variation revealed significant differences in hard coral assemblages between depths (PERMANOVA, all: p =0.001, Table 2.3, Appendix A Figure S2). However, significant depth-by-atoll interactions (PERMANOVA, Pseudo $F_{3, 650} = 7.40$, p = 0.001; Figure 2.4) and dispersion (Appendix A Table S3), indicate the variation in hard coral assemblages between depth varied among atolls across the archipelago, particularly at SA and PB (Appendix A Table S3).



Figure 2.4: Non-metric dimensional scaling (nMDS) of coral genera assemblage, showing clustering by depths, based on Bray-Curtis dissimilarities of square-root transformed data in a total of 26 sites in the Chagos Archipelago. Coloured ellipses represent dispersion of depth centroids at 95% confidence limit – blue: shallow sites (5-10 m) and red: deep site (20-25 m). **Symbols** represent surveyed atolls _ Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Bottom: Vectors represent coral genera distribution to the patterns on the ordination plot.

Table 2.3: Within-atoll variation in the hard coral assemblage between depth using one-way permutational analysis of variance (PERMANOVA) at : Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) in the Chagos Archipelago in 2013. In bold are significant p values. * indicate where zero-inflated generalised mixed effect models were performed. df – degree of freedom, Coeff- coefficient estimates, SE- Standard error.

Atoll	PseudoF-ratio	df	p-value		
EG	17.016	1,116	< 0.001		
GCB	6.494	1,160	< 0.001		
PB	25.461	1,95	< 0.001		
SA	15.150	1,276	< 0.001		

A / 11

Indicator taxa analyses identified a total of 14 coral genera as well as the 'other' category that characterised the hard coral community across all atolls and depth combinations (Figure 2.5, Table 2.5). A higher number of coral genera (10) characterised the deeper reefs than the shallow reefs (6). Coral genera significantly associated with shallow reefs in EG were *Acropora*, *Porites* and *Pocillopora*. Coral genera significantly associated with deep reefs in EG were *Favia*, *Pachyseris* and *Pavona*. *Porites* was the only genus that significantly characterised the shallow reefs in GCB. The hard coral assemblage on deep reefs in GCB was characterised by *Acropora*, *Echinopora*, *Pachyseris* and *Symphyllia*. The shallow reefs of both northern atolls, PB and SA were characterised by *Acropora*, *Pocillopora*, *Porites* and *Stylophora*. In SA, the hard coral community associated with the deep reefs in PB was *Tubastrea*. In SA, the hard coral community associated with the 2.5).

Acropora and *Porites* were the only genera that were consistently associated with both depths across all atolls (Table 2.5). Univariate analyses showed that the cover of *Acropora* decreased with increasing depth at EG and SA (Table 2.4). Increasing depth also had a negative effect on the cover of *Porites* at EG and PB (Table 2.4).



Figure 2.5: Proportional cover (%) of indicator coral genera across atolls: – Egmont (EG); Great Chagos Bank (GCB); Peros Banhos (PB); and Salomon (SA), between depths (5–10 m (grey) and 20–25 m (black)). Indicator coral genera are ranked from the most to the least abundant and were based on their p-values from the indicator species analyses (Table 2.5).

Table 2.4: Within-atoll variation in common indicator coral genera using generalised linear mixed effect models (GLMM) at: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). In bold are significant p values. * indicate where zero-inflated generalised mixed effect models were performed. df – degree of freedom, Coeff- coefficient estimates, SE- Standard error.

Coral genera	Atoll	Effect	Coeff	SE	z-statistics	p-value
Acropora		Intercept	-5.636	0.758	-7.437	< 0.001
	EG	Depth	2.145	0.972	2.208	0.027
Porites		Intercept	-4.725	0.397	-11.900	< 0.001
		Depth	2.113	0.493	4.290	< 0.001
Pocillopora*		Intercept	-1.647	0.239	-6.886	< 0.001
		Depth	-0.285	0.269	-1.058	0.290
Other		Intercept	-3.518	0.267	-13.183	< 0.001
		Depth	0.197	0.369	0.533	0.594
Acropora		Intercept	-2.137	1.101	-1.941	0.052
	GCB	Depth	-1.607	1.608	-0.999	0.318
Porites		Intercept	-4.339	1.090 -3.981		< 0.001
		Depth	1.062	1.490	0.713	0.476
Pocillopora		Intercept	-4.076	0.340	-12.006	< 0.001
		Depth	-0.192	0.475	-0.405	0.686
Other		Intercept	-3.205	0.261	-12.297	< 0.001
------------------------	-----	-----------	--------	-------	---------	---------
		Depth	0.090	0.365	0.248	0.804
Acropora*		Intercept	-2.245	0.776	-2.891	0.004
		Depth	0.491	0.783	0.627	0.531
Porites		Intercept	-4.719	1.041	-4.532	< 0.001
	DB	Depth	3.632	1.341	2.708	0.007
Pocillopora*	I D	Intercept	-1.344	0.259	-5.183	< 0.001
		Depth	-0.707	0.294	-2.407	0.016
Other		Intercept	-4.563	0.430	-10.614	< 0.001
		Depth	1.508	0.531	2.841	0.004
Acropora		Intercept	-3.838	0.625	-6.146	< 0.001
Porites Pocillopora	SA	Depth	1.771	0.865	2.047	0.041
		Intercept	-2.980	0.313	-9.529	< 0.001
		Depth	0.430	0.435	0.989	0.323
		Intercept	-5.288	0.338	-15.627	< 0.001
		Depth	0.987	0.409	2.412	0.016
Other		Intercept	-3.056	0.151	-20.283	< 0.001
		Depth	0.245	0.208	1.175	0.240

Table 2.5: Indicator coral genera at atolls- Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) at shallow (5-10m) and deep (20-25m) sites. `A` represents the specificity of a genera as an indicator of the depth group, `B` is the fidelity of the genera as an indicator of the samples collected within the respective depth group and `sqrtIV` represents the square-root of the indicator value index. The lower and upper confidence interval (CI) were calculated using bootstrapping technique (Cáceres and Legendre 2009).

Atoll	Depth	Coral genera	А	Lower CI	Upper CI	В	Lower CI	Upper CI	sqrtIV	Lower CI	Upper CI	p-value
5 EG 2		Acropora	0.842	0.643	1.000	0.178	0.089	0.267	0.387	0.239	0.475	0.001
	5 10m	Favia	1.000	1.000	1.000	0.056	0.013	0.114	0.236	0.115	0.338	0.029
	5-10m	Pocillopora	0.813	0.600	1.000	0.144	0.073	0.213	0.343	0.221	0.438	0.009
		Porites	0.844	0.737	0.930	0.600	0.482	0.700	0.712	0.610	0.785	0.0001
	20.25-	Pachyseris	1.000	1.000	1.000	0.056	0.011	0.096	0.236	0.103	0.318	0.028
	20-25m	Pavona	1.000	1.000	1.000	0.089	0.037	0.149	0.298	0.191	0.391	0.004
GCB 20-	5-10m	Porites	0.651	0.500	0.762	0.456	0.347	0.567	0.544	0.443	0.636	0.002
		Acropora	0.594	0.479	0.710	0.456	0.347	0.564	0.520	0.419	0.615	0.034
	20.25	Echinopora	1.000	1.000	1.000	0.078	0.030	0.133	0.279	0.177	0.364	0.007
	20-25m	Pachyseris	0.909	0.667	1.000	0.111	0.047	0.180	0.318	0.195	0.411	0.005
		Symphyllia	1.000	1.000	1.000	0.078	0.027	0.133	0.279	0.163	0.364	0.007
PB 5-10m		Acropora	0.970	0.893	1.000	0.533	0.404	0.640	0.719	0.628	0.796	0.0001
		Other	0.763	0.613	0.905	0.483	0.375	0.594	0.607	0.491	0.703	0.0001
	5-10m	Pocillopora	0.846	0.600	1.000	0.183	0.089	0.274	0.394	0.242	0.513	0.008
		Porites	0.873	0.794	0.945	0.917	0.845	0.984	0.895	0.832	0.946	0.0001
		Stylophora	1.000	1.000	1.000	0.150	0.068	0.246	0.387	0.260	0.496	0.001
	20-25m	Tubastraea	1.000	1.000	1.000	0.217	0.120	0.328	0.465	0.346	0.573	0.0003
SA		Acropora	0.696	0.600	0.766	0.580	0.497	0.660	0.635	0.552	0.703	0.0001
	5-10m	Pocillopora	0.694	0.537	0.846	0.167	0.107	0.225	0.340	0.248	0.412	0.009
		Porites	0.573	0.488	0.655	0.473	0.390	0.556	0.521	0.450	0.588	0.021
		Stylophora	0.917	0.769	1.000	0.073	0.039	0.122	0.259	0.186	0.349	0.004
	20.25	Acanthastrea	1.000	1.000	1.000	0.033	0.006	0.070	0.183	0.083	0.270	0.032
	20-25m	Goniastrea	0.917	0.714	1.000	0.073	0.033	0.115	0.259	0.163	0.330	0.004

Montipora	0.727	0.595	0.865	0.160	0.105	0.216	0.341	0.259	0.418	0.005
Pachyseris	1.000	1.000	1.000	0.147	0.086	0.195	0.383	0.292	0.442	0.0001
Seriatopora	1.000	1.000	1.000	0.080	0.041	0.128	0.283	0.203	0.357	0.0002

2.4 Discussion

Our results showed the variation in the benthic community structure of the Chagos Archipelago was driven by significant depth-by-atoll interactions. Although the zonation patterns of the benthic community varied across atolls, a distinct contrast was observed between shallow (5-10 m) and deep (20–25 m) communities, both in terms of the major functional groups and hard coral assemblages, within each atoll. Several earlier coral reef studies report predictable vertical zonation in benthic communities and hard coral assemblages (e.g. Goreau 1959; Done 1982, 1983; Sheppard 1982). However, the among-atoll variation in depth effect observed in this study is consistent with recent research documenting spatial heterogeneity in tropical reefs (Edmunds and Bruno 1996; Williams et al. 2013; Edmunds and Leichter 2016; Karisa et al. 2020; Ford et al. 2020). Spatial variation in depth zonation may be indicative of local biophysical gradients at each atoll that are interacting with depth to structure benthic assemblages (Whittaker 1972; Reice 1994; Vellend 2010). Physical variables that co-vary with depth, such as light (Edmunds et al. 2018), wave exposure (Williams et al. 2013; Gove et al. 2015), reef slope (Sheppard 1982), seasonal thermocline (Kahng and Kelley 2007), resource availability (Fox et al. 2018; Williams et al. 2018), internal wave activities (Leichter and Salvatore 2006; Radice et al. 2019), and disturbance history, e.g. storms (Hughes and Connell 1999) and climate-induced bleaching events (Bridge et al. 2014a, b; Adjeroud et al. 2018), have been shown to influence reef communities.

The distinct variation in benthic composition across depth within each atoll, is comparable to changes with depth in several other Indo-Pacific locations: Central Pacific Kingman and Palmyra atoll (Williams et al. 2013), French Polynesia (Edmunds and Leichter 2016), New Caledonia (Adjeroud et al. 2019), the Maldives (Ciarapica and Passeri 1993), and Kenya (Karisa et al. 2020). Coral genera that consistently associated with shallow reefs were *Acropora, Pocillopora* and *Stylophora*. These coral genera frequently exhibit arborescent and bushy morphologies in shallow areas (Sheppard 1982) and have better light-scattering properties (Titlyanov and Titlyanova 2002; Marcelino et al. 2013). They are therefore better adapted to the high light regimes that can be experienced in shallow reef environments (Hoegh-Guldberg and Jones 1999; Winters et al. 2003). These species also have effective mechanisms, such as polyp inflation, tentacular action and mucus production to shed sediment particles that are resuspended due to wave action (Erftemeijer et al. 2012; Duckworth et al. 2017) at highly exposed shallow reefs (Fulton et al. 2001).

Pachyseris, Pavona, Echinopora, Acanthastrea, Goniastrea, Montipora and Symphyllia were characteristic of the hard coral assemblage on deep reefs. These coral genera frequently adopt foliose, encrusting and massive growth forms on deeper forereef slopes (Sheppard 1982). As irradiance levels decrease with increasing depths, morphological adaptations including the development of larger surface areas, such as foliose and encrusting growth forms, help increase efficiency in light capture to optimise photosynthetic activities (Done 1983; DiPerna et al. 2018). Foliose and massive species also contain higher densities of photosynthetic dinoflagellates (Symbiodinium) for maximising food production in low light regimes (Li et al. 2008). Many of the deeper dwelling massive and sub-massive species exhibit heterotrophic traits; with larger polyp sizes and longer tentacles to allow energy requirements to be met by zooplankton feeding (Hoogenboom et al. 2015; Tremblay et al. 2015). The occurrence of the azooxanthellate Tubastrea as a characteristic coral genera across the deep overhangs of the northern atoll, PB (Andradi-Brown et al. 2019) provides evidence of the presence of highly productive waters in the area. We hypothesise that that the deeper forereef areas of the archipelago are more likely recipient of cooler, nutrient-rich upwelling waters than shallow reef areas (Sheppard 2009; Sheppard et al. 2017).

Acropora and *Porites* characterised both shallow and deep forereef slopes across all atolls. Previous studies in the Chagos Archipelago have also highlighted the dominance of these two coral genera at both shallow and deep forereef slopes (Sheppard et al. 2008a). These typically depth generalist genera contain large numbers of species (Veron et al. 2019) that have different physiological and phenotypical traits which give them the ability to persist in diverse environments across depth gradients (Toda et al. 2007; Darling et al. 2012). Both genera have high larval dispersion rates facilitating settlement across depths (Holstein et al. 2016; Serrano et al. 2016). *Acropora* and *Porites* have been found to host diverse endosymbionts to optimise photosynthesis in decreased light (Muir et al. 2015; Ziegler et al. 2015; Tan et al. 2020). *Acropora* are often characterised as a fast growing weedy species which have overtopping abilities and can encroach neighbouring species (Riegl and Purkis 2009). *Porites* with massive morphologies can grow taller and larger, and physically outcompete other surrounding species (Potts et al. 1985).

Increasing depth had a positive effect on turf algae at PB and CCA cover at EG. Several previous studies have found that turf algae and CCA were more abundant in shallow reef environments (Williams et al. 2013; Marlow et al. 2019; Karisa et al. 2020). The high cover of turf algae and CCA we observed at deep forereef slopes of the Chagos Archipelago may be

related to the grazing pressure across depth (Heenan and Williams 2013). Intensive herbivory promotes the removal of epiphytic turf algae (Rasher et al. 2012; Osuka et al. 2018; Roff et al. 2019) and provides space for the growth of the rapid colonising CCA (Airoldi 2000; Russell 2007). Within EG, high grazing intensity coupled with elevated herbivore and excavator biomass between 8–17 m, were associated with CCA dominated habitats on forereef slopes (Samoilys et al. 2018; Sheppard et al. 2013b). A lower biomass of herbivorous fishes has also been reported on the deeper forereefs of the Chagos Archipelago (Andradi-Brown et al. 2019), which could potentially explain the observed higher turf cover on the deep reefs of PB.

Among all measured major functional groups, dead coral was the only group which had consistently higher cover in shallow forereef slopes across all atolls. During the 1998 massive bleaching events, all shallow ocean-facing reefs in the Chagos Archipelago were highly impacted, leaving large quantities of dead corals (Sheppard, 1999). Several subsequent bleaching events in shallow waters in the 2000s also resulted in localised mortality (Harris and Sheppard 2008; Sheppard et al. 2008), which may have inhibited recruitment and growth, explaining the higher dead coral cover at 5–10m across the archipelago.

Soft coral and sponge cover increased with depth, notably at EG and PB. Previous findings in Indo-Pacific reef systems (Reichelt et al. 1986; Barnes and Bell 2002), including the Chagos Archipelago (Sheppard 1981; Schleyer and Benayahu 2010) show similar increase in soft coral and sponge cover with depth. Sponges and soft corals species have phototrophic, heterotrophic and mixotrophic abilities (Wilkinson 1983; Fabricius and Klumpp 1995). Their high cover in deeper forereef can result from photoadaptation of autotrophic species to increased depths (Fabricius and De'ath 2008; Shoham and Benayahu 2017). Mixotrophic and heterotrophic sponges and soft corals can feed from large flows of inorganic nutrients that are delivered by cold water upwelling and/or internal waves that occur on deeper reef sites (Lesser 2006; Pupier et al. 2019). Deep steep walls are also less prone to sedimentation creating favourable habitat for octocorals (Bridge et al. 2011b). Accentuated by the steep walls of deep sites of PB (Sheppard 1980; Winterbottom et al. 1989), deep rich waters may upregulate heterotrophic feeding in soft corals and sponges, explaining the observed higher cover in its deep forereef slopes (Schleyer and Benayahu 2010; Sheppard et al. 2013b).

It is important to understand the reef community composition of the Chagos Archipelago in the context of disturbances that have affected its reefs. Classic ecological theories suggest that following a disturbance, communities undergo secondary succession (Horn 1974). A major disturbance event prior to 2013 was the pan tropical bleaching event in 1998 (Wilkinson et al.

1999). Previous studies provided evidence that the benthic community of the Chagos Archipelago has transitioned through different successional stages since the 1998 bleaching event. A recovery occurred from minimal hard coral cover (~12% in 1999; Sheppard, 1999) to a coral-dominated community where no significant divergence was apparent in 2012, relative to the pre-1998 community (Sheppard et al. 2008, 2013b). Despite the overall reassembly towards a coral-dominated reef, there was significant variability in benthic community recovery, across depths and atolls (Sheppard et al. 2008). In 2001, less degradation was observed in deep sites of the northern atolls (PB and SA) (high mortality observed at <10-15 m) while the southern atolls (GCB and EG) showed significant mortality at depths >35 m (Sheppard et al. 2002). In 2006, the hard coral assemblages in shallow sites (4–10 m) recovered faster than deep forereef slopes (20-25 m) across PB, SA and GCB, with the exception of EG where no recovery was observed at either depth (Sheppard et al. 2008). In 2012, a general decrease in hard coral cover and increase in sponge and soft coral cover could be observed with increasing depth (5–25 m) across the archipelago (Sheppard et al. 2013b). This rapid recovery in shallow sites (8–10 m) may be driven by the high growth rates in Acropora-dominated shallow communities within the archipelago (Perry et al. 2015).

Our results reveal the spatial variation in depth zonation of benthic communities, potentially linked to previously described biophysical gradients occurring across these depths and atolls (Sheppard 2009; Fasolo 2013; Sheppard et al. 2017). These benthic community data from 2013 will provide insights into the impact of the 2014–2017 back-to-back bleaching events as well as subsequent recovery. It is becoming more important to understand the spatial variability in reef ecosystems in order to infer and predict how communities might respond to the effects of increasing disturbances (Bridge et al. 2014b; Hughes et al. 2019). There is therefore a need to incorporate spatial variation in depth effect within ecological studies, as contemporary shallow reefs are changing rapidly across depths.

Chapter 3: Depth variation in benthic community response to repeated thermal stress on remote reefs

Abstract

Coral reefs are increasingly impacted by climate-induced warming events. However, there is limited empirical evidence on the variation in the response of shallow coral reef communities to thermal stress across depth. Using benthic community data before and after the 2015–2017 successive marine heatwaves, we assess depth-dependent changes in coral reef benthic communities, across a 5–25 m depth gradient in the remote Chagos Archipelago, Central Indian Ocean. Our analyses show an overall decline in hard and soft coral cover and an increase in crustose coralline algae, sponge and reef pavement following successive marine heatwaves in a remote reef system. Our findings indicate variable benthic group cover found at shallow (5–15 m) than at deeper (15–25 m) reef zones. The loss of hard coral cover was better predicted by initial thermal stress, whilst the loss of soft coral was associated with repeated thermal stress following successive warming events. Even if impacts might reduce with depth, our study shows that benthic communities extending to 25 m were impacted by successive marine heatwaves, supporting concerns about the resilience of shallow coral reef communities to increasingly severe climate-driven warming events.

In revision

Sannassy Pilly S et al, 2023. Depth variation in benthic community response to repeated thermal tress on remote reefs, Royal Society Open Science.

3.1 Introduction

Climate-induced thermal stress is one of the main drivers of change in coral reef benthic communities (Hughes et al. 2017b; Lough et al. 2018; Oliver et al. 2018a). However, the degree to which disturbance events affect ecological communities is not uniform across space and varies along environmental gradients (Schwartz et al. 2015; Blowes et al. 2019; Giraldo-Ospina et al. 2020). Coral reefs show significant spatial and temporal heterogeneity in community structure post-disturbance (Bridge et al. 2013; Adjeroud et al. 2018; Baird et al. 2018). Whilst most assessments of the extent of coral bleaching, and consequent degradation and succession processes are carried out in shallow depths (2-10 m) of tropical reef systems (Perry and Morgan 2017b; Hughes et al. 2018a; Elma et al. 2023), the response of shallow benthic communities to thermal stress across the extent of their depth range (0-30 m) is poorly described. As light, temperature (Kahng et al. 2019) and waves decrease with increasing depth, and the availability of organic resources increases at depths (Lowe and Falter 2015; Williams et al. 2018), it is expected that the response of benthic communities to thermal stress will dampen (Glynn 1996). However, contrary to the deep reef refugia hypothesis, which suggests that reefs at greater depths could escape the effects of climate-induced bleaching events (Glynn 1996; Bak et al. 2005), increasing evidence of bleaching and mortality at shallow (2–27 m) and mesophotic depth zones (\geq 30 m) (Smith et al. 2016; Sheppard et al. 2017; Muir et al. 2017; Morais and Santos 2018; Schramek et al. 2018; Frade et al. 2018; Baird et al. 2018; Crosbie et al. 2019; Venegas et al. 2019) underlines the necessity to assess communities across larger depth gradients. Additionally, the limited overlap of species between shallow and deep reefs (Rocha et al. 2018; Roberts et al. 2019) and significant genetic divergence between species across depths indicate that deeper populations may not always provide viable propagules to repopulate shallow reefs (Brazeau et al. 2013; Bongaerts et al. 2017). These observations have important implications for coral reef assessments that evaluate the ecological response of shallow reef organisms to increasingly frequent thermal stress events, which are predicted to occur annually by 2050 (van Hooidonk et al. 2016).

In 2014–2017, the world observed the first back-to-back coral bleaching events that were documented over three years (Heron et al. 2016; Genner et al. 2017; Eakin et al. 2022). The recurring heatwaves caused coral bleaching on 80% of coral reefs globally and mass mortality of corals (Eakin et al. 2017; Hughes et al. 2017b, 2018a; Eakin et al. 2022). Thermal anomalies such as the 2014–2017 warming events have raised global concern about the resilience and persistence of tropical reef systems (Hughes et al. 2017b; Eakin et al. 2022). Chronic disturbances can impede recovery and induce significant degradation in communities (Connell

1997). As the increased intensity and frequency of ocean-warming events (Donner et al. 2017; Hughes et al. 2018b; Frölicher et al. 2018) shorten the recovery window for benthic communities (Osborne et al. 2017; Oliver et al. 2018b; Head et al. 2019b), they can lead to potentially irreversible ecological changes (Gilman et al. 2010; Schmitt et al. 2019).

Large scale bleaching-induced coral mortality on coral reefs alters the dynamic interactions between benthic groups causing significant shifts in community assemblages (Dornelas et al. 2014; Reverter et al. 2022). Whilst the loss of hard corals can cause bare reef pavement to dominate the substrate (Benkwitt et al. 2019; Lange et al. 2021), ecological regime shifts on coral reefs can generate non-coral dominated states primarily characterised by benthic taxa such as algae (including crustose coralline algae, turf and macroalgae), soft corals and sponges (Wee et al. 2017; Bell et al. 2018; Courtney et al. 2022; Reverter et al. 2022; Tebbett et al. 2023; Cornwall et al. 2023). Opportunistic and faster growing in nature, these alternate benthic groups competitively replace hard corals, which can lead to a loss of complexity (Magel et al. 2019; Elliott et al. 2018), reduce reef carbonate budgets (Molina-Hernández et al. 2020; Cornwall et al. 2021), and alter reef-associated fish communities (Richardson et al. 2018; Robinson et al. 2019b), resulting in a decline in the provision of important ecosystem services (Woodhead et al. 2019; Eddy et al. 2021). In some instances, coral reef communities can undergo succession until they reassemble a hard coral dominated assemblage similar to their pre-disturbance state, but characterised by an altered coral community composition (Adjeroud et al. 2018; Darling et al. 2019; González-Barrios et al. 2021).

Whilst climate-driven community changes may result in degraded and less resilient reefs (Schramek et al. 2018; McWilliam et al. 2020), the depth variability in changes in benthic community assemblages is poorly understood. Coral reef benthic communities are highly heterogeneous (McClanahan et al. 2014; Ford et al. 2020) and naturally show diverse vertical zonation patterns (Edmunds and Leichter 2016; Roberts et al. 2019; Sannassy Pilly et al. 2022) as a result of the interaction between biophysical processes that concomitantly vary across depth (Levin 1992; Williams et al. 2018; Spring and Williams 2023). During a marine heatwave, modifications in physiologically important factors such as the combination of sustained elevated seawater temperatures and high solar radiation are often the main causes of bleaching and degradation on reefs (Glynn 1996; McClanahan et al. 2009; McClanahan 2020). Additionally, the proportion of change in benthic communities following a marine heatwave may be due to the assemblage composition (Hughes et al. 2018a). Studies show that coral species have different thermal tolerance (Marshall and Baird 2000; Dalton et al. 2020;

McClanahan et al. 2020) and the susceptibility of species within the same genus to climateinduced bleaching can vary significantly across depth (Muir et al. 2017). In addition, imports of nutrient rich and cold water from deep-water upwelling and internal waves onto shallow reef systems can confer resilience to change in ecological communities during ocean warming events (Reid et al. 2019; Fox et al. 2023). It is therefore expected that the response of benthic communities to thermal stress and the subsequent change in zonation patterns to vary across the water column (Bridge et al. 2014a, b; Muir et al. 2017).

Where post-bleaching coral reef assessments incorporate multiple depth zones, they can estimate depth dependent mortality, identify surviving populations with the potential to repopulate (Bridge et al. 2014a; Muir et al. 2017) and provide a better understanding of the trajectory of community changes across the extent of shallow reef systems (0–30 m) (Bridge et al. 2014a; Muir et al. 2017; Crosbie et al. 2019; Sheppard et al. 2020). Here, we use benthic community surveys from shallow forereefs of the remote Chagos Archipelago, Central Indian Ocean, before and after successive marine heatwaves in 2015–2017, to investigate the effects of recurrent severe thermal stress on the change in benthic communities across a depth gradient of 5–25 m. In 2015–2017, the marine heatwave caused severe coral bleaching and mortality in the Chagos Archipelago, with sustained declines in coral cover due to two consecutive years of elevated temperature stress (Head et al. 2019b). Specifically, we assess the change in composition of those groups across depths at four atolls in the archipelago. We also examine differences between initial and repeated effects of thermal stress on the observed changes in benthic composition.

3.2 Materials and Methods

3.2.1 Study Sites

The Chagos Archipelago is a remote archipelago located in the Central Indian Ocean. Situated at the southern end of the Laccadives-Maldives-Chagos ridge, it covers a total area of 640 000 km² and consists of five islanded atolls. The archipelago has been uninhabited since the early 1970s, except for the US military base on the southern atoll, Diego Garcia (Sheppard 1999b). Benthic community data were collected with repeat sampling, in 2013/2014 (before) and 2018/2019 (after) following successive severe marine heatwaves in 2015–2017 from 16 sites on forereef slopes across four atolls: Peros Banhos (PB), Salomon (SA), Great Chagos Bank (GCB) and Egmont (EG) (Figure 3.1). Surveys in each period were carried out in March-April

and conducted at four depth zones: 5-10 m, 10-15 m, 15-20 m, and 20-25 m. For ease of interpretation, shallower depth zones in text refer to benthic groups occurring between 5-15 m and deeper zones to benthic groups occurring between 15-25 m.



Figure 3.1: Map of sampled sites (red points) around surveyed atolls (in bold) in the Chagos Archipelago – northern atolls: Peros Banhos, Salomon and southern atolls: Great Chagos Bank and Egmont - see Appendix B Table S1 for list of sites and coordinates.

3.2.2 Data collection and benthic community assessment

Benthic community assessment was carried out using 10 min continuous video swims conducted at each site and depth zone. Equipped with two spotlights and two red laser pointers set at 10 cm apart, the camera set-up provided a scale of measurement of the benthos and adjustment for lower light levels at greater depth. During the survey, the camera was held approximately 0.5 m above the substrate and at a 45° angle to capture benthic organisms and

substrate types under overhangs and canopies (Goatley and Bellwood 2011). Each video was converted into a sequence of still images (25 frames per second in Pinnacle Studio, v22.2.0). Thirty of these images per depth zone per site were selected for analysis using Matlab (R2018a.Ink) (total across all sites, n = 5610). Selected images were separated by 80–100 frames in each sequence to avoid re-sampling the same area of reef.

Benthic composition within each image was quantified using Coral Point Count with excel extensions (CPCe) (Kohler and Gill 2006). To reduce observer bias, image analysis was equally distributed among SSP, RR, and LR (10 images per person per site). Percentage cover of benthic organisms and other substrate types was quantified at 15 randomly allocated points on each image, using a stratified random design (Suchley 2014). The broad classification of benthic groups was adapted from Denis et al. (2017) and the NOAA Coral Reef Information System (NOAA 2014). This study examined five benthic groups that have been found to undergo shifts in dominance on coral reefs following thermal stress events: hard coral, soft coral, sponge, crustose coralline algae (CCA) and reef pavement (Chaves-Fonnegra et al. 2018; Cornwall et al. 2019; Slattery et al. 2019; Carballo-Bolaños et al. 2020; Lange et al. 2021). Unlike other Caribbean and Indo-Pacific region, the Chagos Archipelago do not show increase in macroalgae cover

3.2.3 Estimating change in benthic groups following 2015–2017 bleaching events

The change in benthic group cover which occurred before and after the 2015–2017 warming events was calculated using:

- -

$$\delta = \frac{\log\left(\frac{V_f}{V_0}\right)}{t},$$

where δ is the geometric logarithmic change in cover, V_f is the percentage cover of benthic group collected at the end of the time series, i.e., 2018 or 2019 (hereinafter post-heatwaves), and V_0 is the percentage cover of benthic groups at the beginning of the time series, i.e., 2013 or 2014 (hereinafter pre-heatwaves), and *t* is the duration of the time in years between benthic surveys, i.e., before and after the successive marine heatwaves (Côté et al. 2005). This approach optimised the dataset by including surveyed sites that were monitored in different years before and after the heat stress event, i.e., to include pre-disturbance community data collected in 2013 or 2014 (pre-heatwaves), and post-disturbance community data sampled in 2018 or 2019 (postheatwaves). By scaling the post-heatwave cover (V_f) with respect to the pre-heatwave (V_0) cover across sites and depth zones, the change in benthic cover that is inherently variable among sites and depth zones can be compared (Côté et al. 2005). The geometric logarithmic change in cover metric allows the quantification and comparison of non-linear time series by taking into consideration the exponential decline and increase in cover of benthic communities over time and produces similar rates for declines and matching increases. (sensu Côté et al., 2005), (see example: Côté et al. 2006; González-Barrios et al. 2021). To summarise the geometric logarithmic change in cover metric, a negative value represents a loss in benthic group cover form pre- to post-heatwaves and a positive value indicates an increase in benthic group cover following thermal stress. Variation in the change in benthic group cover across depth zones was visualised using a forest plot (ggplot: ggplot2 package, (Wickam 2016)). For ease of interpretation, the log change in cover was back transformed to percentage change in cover (Figure 3.3), using:

$$i = (e^{\delta} - 1) \times 100,$$

where δ is the geometric logarithmic change in cover and i is the percentage change in cover.

3.2.4 Exposure to repeated thermal stress

To determine how benthic groups were affected by thermal stress across depth zones during the 2015–2017 marine heatwaves, maximum degree heat week (hereinafter maxDHW) was used to quantify thermal anomalies from 2015–2017. DHW is a proxy for accumulated thermal stress, represented by a 1°C increase above the local mean climatic temperature over a 12-week period at a given pixel and expressed as degree Celsius weeks (°C-weeks); and maxDHW is the annual maximum accumulated thermal stress in a year. Using the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch 5 km resolution product (NOAA Coral Reef Watch 2018), the annual maxDHW between January 2015 and December 2017 was extracted for each study site (using R packages: ncdf4 (Pierce 2021), raster (Hijmans 2021), rgdal (Bivand et al. 2021) and sp (Pebesma and Bivand 2005)). A DHW threshold of 4°C-weeks may be indicative of significant coral bleaching, and a DHW value of 8°C-weeks is a signal for severe and widespread bleaching with likely mortality (Liu et al. 2014; Hughes et al. 2018a; Claar et al. 2018; Harrison et al. 2019; Ceccarelli et al. 2020).

The peaks of marine heatwave events occurred between May–June 2015 ($4.24 \pm 0.35 - 6.13 \pm 0.26$ °C-weeks) and April–June 2016 ($12.14 \pm 0.08 - 15.84 \pm 0.06$ °C-weeks) (Figure 3.2) Here, initial thermal stress refers to maxDHW recorded in 2015 in the first year of the successive severe heatwaves and repeated thermal stress refers to the cumulative maxDHW recorded in all years from 2015–2017 (Appendix B Table S1). Local-scale hydrodynamics for e.g. upwelling and changes in mixed layer depth can influence temperature regime across depth gradients (Guillaume-Castel et al. 2021; Diaz et al. 2023b). However, in the absence of depth-specific temperature data from in-situ loggers across all study sites, DHW that were derived from SST was used as a measure of thermal stress experienced at the study sites during the warming events.



Figure 3.2: Peaks of thermal stress indicated by monthly maximum Degree Heating Week (maxDHW) during the 2015–2017 recurring warming events at each atoll: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

3.2.5 Data Analysis

Non-metric multidimensional scaling analysis (nMDS: vegan package; (Oksanen et al. 2012b)) was used to visualise variation in benthic community composition across and within-depth zones among atolls before and after the thermal stress. Using a Bray-Curtis distance of square root transformed data (De Cáceres et al. 2013), the nMDS was computed on 3 dimensions (k

=3) with a stress value of <0.1. A scree plot and a Shepard stress plot were used to assess the ordination stress and the correlation between the original dissimilarity matrix and the distances on the final nMDS plot. Vectors of the different benthic groups were fitted to show their correlations with how atolls and depth zones are clustered on the ordination plots (envfit: vegan package; with 9999 permutations).

A three-way nested permutational multivariate analyses of variance (PERMANOVA) was carried out to assess whether benthic community composition varied across depth zones (4 levels; fixed factor) among atolls (4 levels, fixed factor), and whether variation was observed before and after the successive heatwaves (2 levels; fixed factor), including an interaction term between depth zone, atoll, and heatwave period (i.e., pre and post heatwaves). Sites (random factor) were nested in atolls to account and control for site-specific variation in benthic communities to isolate effects of the fixed factors. Multivariate homogeneity tests identified whether there were differences in benthic community dispersion across depth zones before and after successive heatwaves (betadisper: vegan package, using Bray-Curtis distances between samples). The difference between the mean dispersion in benthic communities before versus after the successive heatwaves across depth zones was tested using a permutation test (permutest: vegan package, with 9999 permutations). Where a significant interaction between depth zones, atolls and successive heatwaves were found, Bonferroni pairwise comparisons of group mean differences were also performed to contrast pre- and post-heatwave communities within depth zones and among atolls.

Bayesian hierarchical models were used to assess the effects of initial and repeated thermal stress on the change in cover of each benthic group (hard coral, soft coral, sponge, CCA and reef pavement) across depth zones and among atolls (brm: brms package, (Bürkner 2018)). A generalised linear mixed effects framework was used to model change in cover (response variable), with a Gaussian distribution, as a function of depth zone, atolls, and initial and repeated thermal stress (population-level effects), with an interaction between depth zone, atoll, and each thermal stress variable. Site (group-level variable) was nested in atoll to control for the spatial variation in the change in benthic groups at the site level. The models were run in Stan (brms package), using weakly informative priors for the regression parameters in the model (Appendix B Table S2). Models were fitted with 2000 iterations across 4 chains, using a Markov Chain Monte Carlo (MCMC) algorithm. Excluding 1000 warm-up iterations per chain, all posterior sampling included 4000 draws to simulate the response variables. Predictors (initial and repeated thermal stress) were centered and the convergence of the MCMC

algorithm was visually assessed using traceplots. Effective and reliable sampling of the posterior distributions were assessed using Gleman-Ruban convergence R-hat values of < 1.05 and a minimum effective sample size (ESS) of > 1000 for all parameters (Gelman et al. 2013). Posterior predictive checks were used to assess model fits (bayesplot package (Gabry and Mahr 2017) and tidybayes package (Kay 2022)). The influence of each predictor (depth zone, atoll, initial and repeated thermal stress) on the change in benthic group cover following the successive severe marine heatwaves was assessed using average marginal effects (emmeans, emtrend: emmeans package, (Lenth 2022)). Uncertainty related to the models' posterior estimates was interpreted with 50% and 95% credible intervals. Strong and weak evidence of change was interpreted when 95% and 50% of the intervals did not intercept zero, respectively (Robinson et al. 2019a; González-Barrios et al. 2021). All data analyses were performed using R 3.5.1 (R Development Core Team 3.5.1 2018).

3.3 Results

3.3.1 Variation in benthic community composition after 2014–2017 marine heatwaves

Multivariate analyses showed no interaction effect between depth and atoll on benthic communities but revealed significant depth-dependent and atoll-dependent variation in benthic community composition before versus after the successive heatwaves across all 16 study sites (Figure 3.3, Table 3.1). These findings indicate that the variation in benthic communities before versus after the marine heatwaves across depth zones did not vary across atolls; and that the difference in benthic groups following the marine heatwaves across atolls did not vary across depth zones. Pairwise comparisons showed significant differences in benthic communities before and after the successive heatwaves across all depth zones, except at 20–25 m, and across all atolls, except at Egmont (Appendix B - Figure S1, Table S3). Dispersion analyses revealed similar dispersion means for benthic communities pre- and post-heatwaves across all depth zones and atolls (Table 3.1).

Table 3.1: Variation in benthic community before and after the 2015–2017 marine heatwaves using permutational analysis of variance (PERMANOVA) and dispersions tests a) across depth zones and b) among atolls within-depth zones: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Pairwise comparisons show significant differences in dispersion means a) across depth zones b) among atolls within depth-zones.

	PERMAN	IOVA		Dispersion		
	Df	Pseudo-f	p-value	Df	Pseudo-f	p-value
Heatwaves x Depth x Atoll	9,127	0.72	0.8274			
Heatwaves x Depth	3,186	5.98	0.0001	7,120	0.4958	0.8361
Heatwaves x Atoll	3,186	5.64	0.0001	7,120	1.0796	0.3807
Depth x Atoll	9,186	1.5796	0.0607			



Figure 3.3: Non-metric multi-dimensional scaling plots (nMDS) of benthic groups from 16 sites in the Chagos Archipelago, showing clustering of communities in 2013/14 (pre) and 2018/19 (post) following the 2015–2017 marine heatwaves across depth zones (green: 5–10 m, orange: 10–15 m, blue: 15–20 m and pink: 20–25 m) at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA), based on Bray-Curtis dissimilarities of square-root transformed data. Ellipses represent dispersion of pre (grey lines) and post (black lines) marine heatwaves communities from centroids at 95% confidence intervals. Vectors show benthic groups that significantly contributed to the patterns on the ordination, arrows show the direction of the gradient, and the length of the vectors are proportional to the correlations between the benthic group and the ordination. Depth-dependent and atoll-dependent variation in benthic communities can be viewed in Appendix B Figure S1.

3.3.2 Depth-dependent temporal change in benthic composition

3.3.2.1 Decline in hard and soft coral cover

Our results revealed an overall decline in hard coral (-14.06 \pm 1.48 %) and soft coral cover (-23.14 \pm 3.09 %), which varied across depth zones and atolls following the 2015–2017 marine heatwaves. Hard coral cover declined at all depth zones (5–25 m) at Great Chagos Bank compared to Egmont where a small gain was observed (Figure 3.4, Appendix B Table S4, Figure S2). The loss in hard coral cover after bleaching was greatest at 5–10 m at Great Chagos Bank (Figure 3.4, Appendix B Table S4) and declined with increasing depth (Figure 3.4, Appendix B Table S4). The loss in soft coral cover was greatest at 5–10 m at all three atolls and became less pronounced with increasing depth (Figure 3.4, Appendix B Table S4). There was a weak negative effect of depth on the loss in soft coral cover at the deeper zones (10–15 m, 15–20 m and 20–25 m) at Peros Banhos and Salomon. There was also a weak negative influence of depth on the decline in soft coral cover at 10–15 m at Great Chagos Bank and at 15–20 m at Egmont (Figure 3.4, Appendix B Table S4).



Figure 3.4: Predicted mean change in benthic groups cover following the 2015–2017 marine heatwaves across depth zones: 5–10 m, 10–15 m, 15–20 m, 20–25 m, and atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Predicted means were generated from posterior predictions. See Appendix B Table S4 for variation (mean \pm SE) in change in benthic groups among atolls across depth zones and Appendix B Figure S1 for percentage cover of benthic groups pre- and post-heatwaves.

3.3.2.2 Increase in CCA, reef pavement and sponge cover

There was an overall 6.58 ± 1.66 % increase in CCA cover following successive heatwaves. There was no evidence of a depth effect on the change in CCA cover post-heatwaves across depths at any atoll, except for an increase in CCA at Great Chagos Bank at 5–10 m and a loss in CCA cover at 20–25 m at Peros Banhos (Figure 3.4, Appendix B Table S4).

Reef pavement increased by 13.39 ± 1.69 % post-heatwaves. The increase in reef pavement at 5–10 m was more pronounced at Egmont and Great Chagos Bank (Figure 3.4, Appendix B Table S4). All atolls showed an increase in reef pavement at 10–15 m (Figure 3.4, Appendix B Table S4). There was a weak positive influence of depth observed on the increase in reef pavement at Egmont and Salomon at 15–20 m (Figure 3.4, Appendix B Table S4). There was a weak positive effect of depth at 20–25 m at Egmont, corresponding to an increase in reef pavement after the thermal stress events (Figure 3.4, Appendix B Table S4).

There was an increase in sponge cover $(24.06 \pm 7.59 \%)$ following successive heatwaves. A weak positive effect of depth was observed at all atolls at 5–10 m and at 10–15 m at Egmont and Great Chagos Bank on the increase in sponge cover post-heatwaves (Figure 3.4, Appendix B Table S4). Sponge cover increased at depths of 15–20 m at Great Chagos Bank, however there was no change in sponge cover at depth of 20–25 m at any of the atolls (Figure 3.4, Appendix B Table S4).

3.3.3 Effects of thermal stress on change in benthic communities across depth zones

Variable effects of initial and repeated thermal stress were observed on the change in benthic groups across depth zones and among atolls. The loss in hard coral cover at all depths was driven by initial thermal stress, with consistent weak negative effects on the decline in hard coral cover across depth zones (Figure 3.5a, Appendix B Table S5). Stronger evidence of hard coral cover loss due to initial thermal stress was shown at Great Chagos Bank across all depth zones, with less pronounced effects at Peros Banhos and Egmont (Figure 3.5b, Appendix B Table S5). Repeated thermal stress had a marginal effect on the decline in hard coral cover across all depth zones. These effects were more pronounced at Great Chagos Bank in deeper zones (10–25 m) (Figure 3.5b, Appendix B Table S5).





Figure 3.5 : Posterior distributions of the standardised effects of initial and repeated thermal stress on the change in hard coral cover following the 2015–2017 marine heatwaves across: a) depth zones: 5–10 m, 10–15 m, 15–20 m and 20–25 m and b) at atolls Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points indicate median estimates and bars represent 50% and 95% credible intervals. Strong and weak evidence of change in benthic cover are interpreted when 95% and 50% of the intervals do not intercept zero, respectively.

Unlike hard coral, changes in soft coral, CCA, reef pavement and sponge cover following successive marine heatwaves were weakly and variably affected by initial and repeated thermal stress across depth zones and among atolls. Repeated thermal stress had weak negative effects on the loss in soft coral cover at 20–25 m (Figure 3.5a), which was more pronounced at Egmont, Great Chagos Bank and Peros Banhos.(Figure 3.5b) Great Chagos Bank was one of the atolls where both initial and repeated thermal stress marginally influenced the loss in soft coral cover across depth (weak positive effects of repeated thermal stress at 10–15 m and 15–20 mand weak negative effects of initial thermal stress at 5–10 m, 15–20 m, and 20–25 m)(Figure 3.6b, Appendix B Table S5). Soft coral cover marginally declined due t initial thermal stress at 20–25 m at Egmont and at Salomon (Figure 3.6b, Appendix B Table S5).





Figure 3.6 : Posterior distributions of the standardised effects of initial and repeated thermal stress on the change in soft coral cover following the 2015–2017 marine heatwaves across: a) depth zones: 5–10 m, 10–15 m, 15–20 m and 20–25 m and b) at atolls Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points indicate median estimates and bars represent 50% and 95% credible intervals. Strong and weak evidence of change in benthic cover are interpreted when 95% and 50% of the intervals do not intercept zero, respectively.

Initial thermal stress marginally increased CCA cover at 5–10 m (Figure 3.6a), which was more pronounced at Great Chagos Bank (Figure 3.7b, Appendix B Table S5). There was no further evidence of an effect of initial thermal stress at other depth zones and atolls (Figure 3.7b, Appendix B Table S5). Repeated thermal stress marginally increased CCA cover at Peros Banhos at the shallower depth zones (5–10 m, 10–15 m). The effects of repeated thermal stress on the change in CCA cover were divergent at 20–25 m, with a small increase at Great Chagos Bank and and small loss at Peros Banhos (Figure 3.7b, Appendix B Table S5).





Figure 3.7 : Posterior distributions of the standardised effects of initial and repeated thermal stress on the change in crustose coralline algae (CCA) cover following the 2015–2017 marine heatwaves across: a) depth zones: 5–10 m, 10–15 m, 15–20 m and 20–25 m and b) at atolls Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points indicate median estimates and bars represent 50% and 95% credible intervals. Strong and weak evidence of change in benthic cover are interpreted when 95% and 50% of the intervals do not intercept zero, respectively.

Whilst there was no overall effect of initial and repeated thermal stress across depth zones, variable patterns were observed at atoll-level (Figure 3.7a). There was no evidence of an effect of initial thermal stress on the increase in reef pavement at the shallow (5–10 m) depth zones at any atoll. Repeated thermal stress slightly increased reef pavement at 5–10 m at Great Chagos Bank and Salomon (Figure 3.8b, Appendix B Table S5). Both initialand repeated thermal stress marginally increased reef pavement at deeper zones (10–15 m, 15–20 m and 20–25 m) at Egmont, Great Chagos Bank and Salomon (Figure 3.8b, Appendix B Table S5).





Figure 3.8 : Posterior distributions of the standardised effects of initial and repeated thermal stress on the change in reef pavement following the 2015–2017 marine heatwaves across depth zones: a) 5–10 m, 10–15 m, 15–20 m and 20–25 m and b) at atolls Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points indicate median estimates and bars represent 50% and 95% credible intervals. Strong and weak evidence of change in benthic cover are interpreted when 95% and 50% of the intervals do not intercept zero, respectively.

Initial thermal stress marginally increased sponge cover at shallower depth zones (5–10 m, 10–15 m) at Great Chagos Bank and at deeper zones (20–25 m) at Peros Banhos (Figure 3.9b, Appendix B Table S5). A slight increase in sponge cover was observed due to repeated thermal stress at mid-depths (10–15 m, 15–20 m) at Egmont, Great Chagos Bank and Peros Banhos (Figure 3.9b, Appendix B Table S5).





Figure 3.9 : Posterior distributions of the standardised effects of initial and repeated thermal stress on the change in sponge cover following the 2015–2017 marine heatwaves across depth zones: 5–10 m, 10–15 m, 15–20 m and 20–25 m at atolls Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points indicate median estimates and bars represent 50% and 95% credible intervals. Strong and weak evidence of change in benthic cover are interpreted when 95% and 50% of the intervals do not intercept zero, respectively.

3.4 Discussion

Changes in benthic communities in the Chagos Archipelago were depth and atoll dependent following successive heatwaves in 2015–2017. Interactions between depth and thermal stress (initial and repeated) differed among benthic groups, indicating variable benthic community response to elevated seawater temperatures across depth. Results indicate greater changes in benthic group cover at shallower (5–15 m) relative to deeper (15–25 m) reef zones. It is evident that intense ocean warming events such as the successive heatwaves in 2014–2017 (Eakin et al. 2017; Skirving et al. 2019) are changing coral-dominated reefs to alternate configurations, with severe impacts on ecosystem functioning (Hughes et al. 2018a). However, the lack of long-term coral reef studies (Reverter et al. 2022) and the focus of coral bleaching assessment on the shallower depths of tropical coral reefs (≤ 10 m) have limited our understanding of the effects of recurring warming events on the changes in coral reef benthic communities across the depth range of shallow reef systems (Hughes et al. 2017b, 2019; Robinson et al. 2019b; Harrison et al. 2019).

Variation in ecological response to thermal stress across depth

Changes in communities occur as a result of the complex interactions between their habitat, physiological traits and the nature of disturbance events (Connell 1978). Here, the change in benthic communities across depths to 25 m was variably and modestly influenced by both initial and repeated thermal stress following the 2015–2017 marine heatwaves. Recent studies show similar trends of little to no significant interaction between depth and thermal stress in explaining post-heatwave trajectories in benthic communities across depth gradients (Baird et al. 2018; Venegas et al. 2019; Donovan et al. 2021). This pattern may relate to biophysical forcing, such as light (Cooper et al. 2007), temperature, salinity (Kleypas et al. 1999; Kahng et al. 2019) and wave and current regimes (Lowe and Falter 2015; Radice et al. 2019), that simultaneously vary across depth (Bridge et al. 2014a; Muir et al. 2017).

During a global warming event, compositional changes observed in benthic communities occur as a result of thermal stress-related coral bleaching, which is caused by increased seawater temperature and light irradiance. As light intensity and temperature naturally declines with increasing depth (Kahng et al. 2019), lower levels of bleaching and mortality are frequently observed at depth (Baird et al. 2018; Frade et al. 2018; Muir et al. 2017), which could account for the lower change in soft and hard coral cover at 15–25 m compared to the shallower communities at 5–15 m. In addition to the combination of the natural attenuation of light and

temperature with increasing depth, the presence of internal waves may explain the smaller change in benthic community cover at deeper reef zones relative to shallow parts of the reefs. Significant water temperature fluctuations with increasing depth suggest strong internal wave activity in the Chagos Archipelago (Sheppard 2009; Harris et al. 2023). Internal waves which drive deep-water upwelling can significantly decrease thermal stress and mitigate the response of benthic organisms to bleaching events at depth (Wyatt et al. 2020). By cooling temperatures and bringing in allochthonous nutrients from the deep, upwelling can increase productivity on shallow reef systems (Radice et al. 2019). When autotrophy is compromised during a warming event (Lough and Caldwell 2018), upwelling can promote heterotrophy and the survival of mixotrophic organisms such as hard and soft corals (Fabricius and Klumpp 1995; Williams et al. 2018; Fox et al. 2018, 2023).

Despite the variation in the change of benthic groups across depths, we observe a consistent pattern of loss in hard coral and soft coral cover, followed by an increase in CCA, reef pavement and sponge cover across all depth zones. The increase in sponge and CCA cover can also be associated with the increase in the proportion of reef pavement after the marine heatwaves. Mass bleaching events have been shown to induce widespread mortality in hard and soft coral communities (Hughes et al. 2018b; Maucieri and Baum 2021) creating vacant space (Cerruti 2020). Recent studies in the Chagos Archipelago have shown a higher proportion of reef pavement and boring sponge cover on shallow exposed sites after the 2015–2017 marine heatwaves compared to more sheltered sites (Lange et al. 2021). Higher wave energy at shallow depths can increase the susceptibility of benthic groups such as dead hard and soft corals to physical damage and dislodgment (Madin and Connolly 2006), resulting in vacant bare reef pavement and promoting the growth of rapidly colonising and wave tolerant organisms like sponge and CCA (Williams et al 2013, Gove et al, 2015).

Variation in ecological response to initial and repeated thermal stress

a) Change in hard coral cover following bleaching events

Among all surveyed benthic groups, there was a consistent negative effect of initial thermal stress across all depth zones only for hard coral cover. This suggests that the initial effect of thermal stress in 2015 had the largest influence on the observed decline in hard coral cover. In contrast the cumulative effect of repeated thermal stress from 2015–2017 was associated with a smaller decline in hard coral cover. Previous studies in Chagos support these findings with comparable patterns reporting higher coral bleaching and mortality in 2015 despite higher

exposure to thermal stress in 2016 (Head et al. 2019b). Similar trends of lower bleaching and mortality rates in the second year of consecutive coral bleaching events were reported on the Great Barrier Reef (Hughes et al. 2019) and in the Coral Sea (Harrison et al. 2019), even though higher thermal stress was recorded in the second year.

There are several mechanisms which could drive successive bleaching resulting in lower coral mortality. Over the duration of a warming event, hard corals can resist, respond and recover from thermal stress (Darling and Côté 2018; Roche et al. 2018). For example, exposure to the initial warming event in 2015 may have created thermal preconditioning for the remaining live hard coral community to develop resistance to subsequent bleaching (Maynard et al. 2008; Guest et al. 2012). In addition, natural association with (Rowan 2004; Wham et al. 2017) or shifting to thermally tolerant endosymbionts during stress (Jones et al. 2008; Keshavmurthy et al. 2014) can decrease bleaching susceptibility and lower coral cover decline during subsequent warming events.

b) Change in other benthic groups following bleaching events

Unlike the hard coral community, the remaining benthic groups showed weak and variable responses to both initial and repeated thermal stress across depth zones. For example, repeated thermal stress increased soft coral cover loss at 20–25 m, whereas no effects were observed on change in soft coral cover at shallower depths. Studies which have looked at the impact of recurring thermal stress on soft coral communities in the Western and Central Pacific also show similar trends of loss related to repeated bleaching and eventual die-offs (Maucieri and Baum 2021; Slattery et al. 2019; Sheppard et al. 2017). The impact of thermal stress at 20–25 m may relate to lower thermal variability at depths making deeper soft coral communities less resilient to chronic warming (Slattery et al. 2019). In addition soft coral communities at depth could be made of more vulnerable populations like *Sarcophyton* colonies which are known to degrade completely after recurring bleaching events compared to *Lobophytum* and *Sinularia* that are more resistant to bleaching (Slattery et al. 2019; Maucieri and Baum 2021).

Both initial and repeated thermal stress decreased the recovery in sponge cover following the 2015–2017 bleaching event. This effect was most pronounced at shallowest depths (5–10 m). The increase in sponge cover that was found is likely driven by an increase in encrusting boring sponges (Carballo et al. 2013; Chaves-Fonnegra et al. 2018), also observed following the major 1998 bleaching event in the Chagos Archipelago (Sheppard et al. 2002). These bio-eroding

sponges can host *Symbiodinium* spp., which are resistant to bleaching (Fang et al. 2016). This association with thermally tolerant holobionts help the sponges to spread rapidly on stressed and dead corals during warming events (Rützler 2002).

CCA was the benthic group least influenced by initial and repeated thermal stress. Repeated thermal stress marginally reduced the recovery of CCA cover at one atoll (Peros Banhos), and minimal or no effect of initial thermal stress was observed on changes in CCA cover. Recent studies show that CCA have high thresholds to elevated water temperatures (Cornwall et al. 2019). Whilst an acute thermal stress event can significantly reduce photosynthetic rates in CCA, they have the potential to acclimatise to chronic elevated water temperatures and maintain photosynthesis and calcification (Page et al. 2021). In addition to being highly tolerant to heat stress, the increase in CCA cover may relate to their high dispersal rates and ability to spread rapidly on various substrates such as available bare reef substrate, dead coral colonies and coral rubble post-bleaching (Kennedy et al. 2017).

There were variable effects of both initial and repeated thermal stress on the increase in available reef pavement. This is likely linked to the loss of previously dominant hard and soft coral cover following the 2014–2017 marine heatwaves on these reefs. The overall gain in available reef pavement also coincides with an increase in fish community herbivory about 2 years following the warming events (Taylor et al. 2020). By sustaining high levels of grazing on endolithic and epilithic algae following bleaching, herbivores can maintain a high proportion of bare reef pavement (Mumby and Steneck 2008; Taylor et al. 2020).

Benthic community reorganisation following thermal stress

The reorganisation of coral reef benthic communities following a disturbance event depends on the dynamic interaction between the nature (scale and severity) of the disturbance event and the reef community composition (Gouezo et al. 2019). Marine heatwaves have been shown to cause widespread bleaching and mortality of scleractinian corals (Lough and van Oppen 2018; Hughes et al. 2017b). This subsequently modifies the network of interactions between the wider benthic community and can cause coral dominated reefs to shift to reefs with novel alternate configurations (Gudka et al. 2020; Claar et al. 2018; Hughes et al. 2018b, 2017b; Heron et al. 2016). During the 2014–2017 thermal stress events, reefs within the Indian Ocean region that experienced high to extreme levels of bleaching (Gudka et al. 2020) altered to configurations dominated by epilithic algal matrix (e.g. Seychelles Aldabra atoll: 139,140; Kenya, Zanzibar: 141,12) and rubble beds (e.g Maldives: 10).

Despite high bleaching and mortality rates during the successive marine heatwaves in the Chagos Archipelago (Head et al. 2019b), there is no evidence suggesting that changes in benthic groups are indicative of a regime shift following bleaching. This resilience to regime shifts in the Chagos Archipelago may be attributed to: 1) the isolation of the reefs from direct anthropogenic activities (e.g., pollution, eutrophication, sedimentation) might provide some resistance to bleaching-induced mortality (Harrison et al. 2019); 2) local upwelling (Sheppard 2009; Harris et al. 2023; Diaz et al. 2023a) may reduce thermal stress and deliver nutrients required by benthic communities resulting in a less severe change in community structure, especially at depths, following the warming events (Riegl et al. 2019; Fox et al. 2023); 3) high fish biomass (Graham et al. 2013; Samoilys et al. 2018) with strong top-down control maintained by a high herbivore density post-bleaching in the archipelago (Taylor et al. 2020) may reduce the successional dominance of algae on the reefs post-disturbance and provide vacant space for coral recruitment and recovery (Mumby 2009); and 4) the Chagos Archipelago has one of the most diverse coral communities in the Indian Ocean region, which has been associated with resilience and recovery following previous severe bleaching events in the archipelago (Sheppard et al. 2002, 2013b) as well as the Great Barrier Reef, Moorea and Jamaica (McWilliam et al. 2020).

Benthic community recovery, which can take 8–13 years, is usually assessed as the return of cover to pre-disturbance levels as well as the reassembly to similar pre-disturbance taxa relative abundances (Gouezo et al. 2019; Muir et al. 2017; Johns et al. 2014). In keeping with recent studies from the Chagos Archipelago that indicate on-going coral recovery towards prebleaching communities 6 years following the bleaching events (Lange et al. 2022), the data from this study precede with a lack of a shift in dominance 1–2 years post-bleaching. Despite significant bleaching and mortality of key coral species such as *Acropora, Pachyseris, Echinopora, Isopora* and *Galaxea* during the back-to-back bleaching events in the Chagos Archipelago (Head et al. 2019; Sheppard et al. 2017, 2020), new coral recruitment across all morphotypes (branching, massive, encrusting, tabular *Acropora*, branching *Acropora*, massive *Porites*) indicates high recovery potential since 2021 (Lange et al. 2022). This high recruitment rate of different morphotypes could be a source of diversity and resilience (van Woesik et al. 2011; Gilmour et al. 2013)
Depth zonation on coral reefs in warming climate

The recovery trends shown by Lange et al (2022) in the Chagos Archipelago only describe reefs at 8–10 m. Several post bleaching coral reef studies similarly focus on changes occurring shallower than 10 m (Hughes et al. 2017b, 2018c; Perry and Morgan 2017b; Fox et al. 2019; Harrison et al. 2019), limiting our understanding of how deeper reefs react to recurring marine heatwaves. It has been suggested that reefs at greater depths may escape the effects of climate-induced bleaching events (Smith et al. 2014; Bak et al. 2005; Glynn 1996). By surveying shallow reefs over a larger depth gradient, we show the loss of hard and soft coral cover postheatwaves between 15–25 m. Whilst less than the observed changes at shallower 5–15 m depths, our results highlight the benthic communities down to 25 m depth can be impacted by severe heatwaves. This is supported by an increasing number of studies that show reefs at greater depths, including mesophotic reefs (30–150 m) are not immune to thermal stress with widespread evidence of bleaching impacts and change in community composition (Bridge et al. 2013; Smith et al. 2016; Bongaerts et al. 2017; Frade et al. 2018; Morais and Santos 2018; Venegas et al. 2019; Diaz et al. 2023b).

Conclusion

We show that benthic communities across a depth gradient of 5-25 m were affected by thermal stress. The decreasing change in cover of benthic groups with depth highlights the importance of surveying multiple depth gradients when explaining the rate at which communities can be altered after large scale disturbance events. The effects of initial and repeated thermal stress across depths show that even remote reefs that are protected from direct anthropogenic impacts are not resistant to the impacts of elevated seawater temperatures, and subsequent changes in community dynamics and zonation patterns. As the return time between climate-induced warming events becomes shorter, the ability of coral reefs to recover to pre-bleaching levels may become compromised (Hughes et al. 2017b, 2018c; Osborne et al. 2017). Our findings support concerns about the ability of contemporary benthic communities on shallow coral reefs (< 30 m) worldwide to resist and recover from recurrent thermal stress.

Abstract

Carbonate budgets are increasingly being used to assess contemporary geo-ecological functioning of rapidly changing coral reefs. Recurrent climate-driven warming events, which typically induce severe coral bleaching and mortality in very shallow depths on topical reefs, are predicted to cause depth-homogenisation of coral cover and community composition across shallow reef habitats (< 30 m). However, data illustrating how carbonate production changes across depth are generally sparse. This study investigates differences in coral cover, community composition and carbonate production rates between two depths (10 m and 17.5 m) across four atolls in the remote Chagos Archipelago. Our results indicate higher coral carbonate production rates at 10 m depth sites with more abundant medium- and large-sized colonies compared to deeper (17.5 m) sites. Reflecting the natural variation in biophysical factors that drive coral community assemblages across depth, the main carbonate producers at the shallower depth sites comprised of fast-growing, framework-building branching, tabular (mainly Acroporids) and massive (mainly Porites) corals. In contrast, carbonate production at deeper sites was driven by slow-growing, low complexity encrusting and foliose morphotypes at the depths. Comparisons between two census-based methodologies indicate significantly higher carbonate production rates estimated by ReefBudget, most likely due to accurate colony size measurements compared to Monte-Carlo simulation of colony sizes and area-normalised scaling technique in CoralNet. Utilising a dataset from the remote Central Indian Ocean, our results show that 6-7 years after the last major bleaching event in 2015/2016, recovery of shallow reefs has re-instated significant differences in carbonate production between depths at 3 out of 4 atolls. However, slower recovery of branching and tabular corals at Great Chagos Bank indeed suggests that bleaching can cause homogenisation of carbonate production across depth. This study contributes to understanding vertical changes in geo-ecological functioning of shallow coral reefs and support evidence of the magnitude and extent of increasingly frequent and severe climate-induced warming events on shallow coral reefs.

4.1 Introduction

Reef carbonate budgets are a measure of the net balance between carbonate production and erosion on coral reefs (Chave et al. 1972). A positive net balance is necessary for the structural development and maintenance of a functional coral reef framework (Perry et al. 2008). Scleractinian corals serve as coral reef foundation species by providing most of the threedimensional structure, with additional carbonate deposited by crustose coralline algae (CCA) and accumulated from sediment generated by the breakdown of calcifying taxa (Chave et al. 1972; Perry et al. 2012). Erosion on reefs occurs as a result of physical disturbances (cyclones and storms), chemical dissolution and bioerosion by grazing parrotfish and sea urchins, and endolithic macro- and microborers such as sponges, worms and bivalves (Scoffin 1993; Glynn and Manzello 2015). By summing calcium carbonate production and bioerosion, the biological aspects of reef carbonate budgets can serve as a quantitative metric to assess vital reef geoecological functions (Brandl et al. 2019). These functions include the provision of habitat for fish and other reef-associated organisms (Graham and Nash 2013; Ferrari et al. 2018), coastal protection though wave energy dissipation (Beck et al. 2018) and sediment generation to maintain beaches and shorelines (Kench and Cowell 2000; Laing et al. 2020); which in turn affect ecosystem goods and services that coral reefs provide (Kennedy et al. 2013; Woodhead et al. 2019).

Regulated by various biophysical factors, carbonate budgets can vary greatly within and across reefs (Takeshita et al. 2018; Brown et al. 2021; Edmunds and Perry 2023; Kahng et al. 2023). Abiotic variables such as light, temperature, pH, alkalinity, nutrient regime, and aragonite saturation state drive variation in calcification and dissolution rates across reefs (Albright et al. 2016; Januchowski-Hartley et al. 2017; Ross et al. 2019). Larger scale oceanographic forcings such as wave exposure, currents and upwelling alter seawater chemistry through water circulation, import and export materials such as nutritional subsidies and sediments (Falter et al. 2013; Eyre et al. 2014), and are also known to influence reef-building capacity (Wizemann et al. 2018; Lange et al. 2021; Rodriguez-Ruano et al. 2023). In addition to the environmental and oceanographic setting, carbonate budgets are intrinsically driven by reef community composition and abundance of associated organisms. Whilst reefs with few hard corals tend to display low-positive or net-negative budget states as bioerosion from parrotfish, urchins and sponges exceeds carbonate production (Perry et al. 2014; Edmunds and Perry 2023), coral-dominated reefs typically show highly positive net carbonate budgets from corals and coralline algae (Van Woesik and Cacciapaglia 2018; Lange and Perry 2019; Brown et al. 2021; Cornwall

et al. 2023). Additionally, variation in coral population structure, including coral taxa diversity, colony size and morphology drive differences in carbonate budgets across reefs (Carlot et al. 2021; Lange et al. 2022).

Given the natural variation in zonation patterns of coral reef communities (Edmunds and Leichter 2016; Roberts et al. 2019; Sannassy Pilly et al. 2022), that occur as a result of biophysical changes across depth gradients (Levin 1992; Couce et al. 2012; Williams et al. 2018), it can be expected that carbonate production and erosion rates vary across depths (Perry and Alvarez-Filip 2019). Whilst an increasing number of studies are now assessing temporal and spatial changes in reef carbonate budgets, the variability across depth gradients is largely unknown (97% of carbonate budget data are from reefs ≤ 10 m depth, Lange et al. 2020). Coral community assemblages tend to shift as light, temperature, aragonite saturation state and wave exposure attenuate with increasing depth (Roik et al. 2018; Kahng et al. 2019). As coral communities adapt to deeper reef zones, they typically favour slow-growing encrusting and foliose growth forms which optimise light capture (Titlyanov and Titlyanova 2002; DiPerna et al. 2018) compared to exposed shallow areas which are dominated by structurally robust branching and massive species with high calcification rates (Marcelino et al. 2013; Guest et al. 2016). These changes in individual calcification rates and coral abundance can lead to lower community calcification rates and thinner reef framework thickness at deeper depths (Weinstein et al. 2016; Kahng et al. 2023).

Changes in reef carbonate budgets are commonly quantified via census-based approaches such as the *ReefBudget* methodology (Lange et al. 2020). *ReefBudget* quantifies the individual contribution of different functional groups and taxa, including carbonate producers and bioeroders towards net carbonate production (Perry et al. 2008, 2012, 2018). Due to past and on-going degradation of coral reefs worldwide (Hughes et al. 2018a; Williams et al. 2019), there has been an increasing interest in census-based methodologies which provide measures of ecological processes that drive coral reef carbonate budget states (Perry et al. 2012, 2018; Lange and Perry 2019; Brown et al. 2021; Lange et al. 2022). Census-based approaches can be adapted to estimate coral carbonate production from planar photographic or video imagery using the Coral Colony Rugosity Index (CCRI), which converts planar measurements to colony contour lengths (Husband et al. 2022), or *CoralNet*, which assigns area-normalized calcification rates to annotated images (Chan et al. 2021; Courtney et al. 2021). Colony scale conversion metrics (Husband et al. 2022) and area-normalised calcification rates (Courtney et al. 2022), with acceptable error margins for many reefs, are likely comparable to *in-situ*

ReefBudget surveys of carbonate budget estimates (CCRI: $\pm 10\%$ margin of error, *CoralNet*: unknown). Both approaches therefore provide the means to describe reef geo-ecological functions across larger spatial and temporal scales by using readily available digital records (Casella et al. 2017; Rodriguez-Ramirez et al. 2020).

Whilst it is evident that anthropogenic and natural disturbances can significantly alter reef carbonate production and erosion processes (Edmunds and Perry 2023), the magnitude of these changes across shallow reef depths (< 30 m) are poorly described. The lack of data on reef carbonate budgets at depths below 10 m limits our understanding of the spatial consequences of ecological change on contemporary reefs under the current climate regime (Lange et al. 2020). Given increasing evidence of bleaching and mortality across both shallow (2–27 m) and mesophotic depths (>30 m) (Smith et al. 2016; Sheppard et al. 2017; Muir et al. 2017; Morais and Santos 2018; Schramek et al. 2018; Frade et al. 2018; Baird et al. 2018; Crosbie et al. 2019; Venegas et al. 2019), it is reasonable to assume that subsequent alterations in coral reef communities across depth will impact carbonate budgets. Here, we address this knowledge gap by examining differences in primary framework production across depths. Specifically, we compare coral carbonate production rates at shallow (10 m) and moderate (17.5 m) depths on forereefs across four atolls in the isolated Chagos Archipelago and evaluate the importance of coral morphotypes and colony size classes. We also provide the first comparison of coral carbonate production rates estimated using *ReefBudget* and *CoralNet* approaches.

4.2 Method

4.2.1 Study Sites

In this study, coral carbonate production rates were estimated on the forereef slopes of the Chagos Archipelago, a remote reef system located in the central Indian Ocean, about 500 km south of the Maldives. A total of 16 sites (n =4 sites/atoll) were surveyed from December 2021 to January 2022, spanning four atolls: Peros Banhos, Salomon, Great Chagos Bank and Egmont (Figure 4.1, Appendix C Table S1). At each site, data was collected at two depths: 10 m (hereinafter shallow depth) and 17.5 m (hereinafter moderate depth), using 30 photo quadrats (0.5 x 0.5 m area) laid along three 10 m long transects (n =10 photo-quadrats/transect) at each depth.



Figure 4.1: Map of sampled sites (red points) around surveyed atolls (in bold) in the Chagos Archipelago – northern atolls; Peros Banhos, Salomon and southern atolls; Great Chagos Bank and Egmont - see Appendix C Table S1 for list of sites and coordinates.

4.2.2 Benthic community composition

Benthic community composition at each site was assessed using the web-based annotation tool *CoralNet* (Beijbom et al. 2015). Using a stratified random design, 15 points were generated on each photo quadrat to identify benthic groups directly below, including: hard coral, soft coral, crustose coralline algae (CCA), turf, fleshy macroalgae, *Halimeda* spp, sponge, sand, rubble, reef pavement, dead coral, bleached coral and `Other` (comprising zoanthids, bryozoans, ascidians, corallimorphs, anemones, clams, and bivalves). Where benthic group identification was limited due to shadowing or blurriness, the `Unknown` classification was chosen. The `hard coral` group was further distinguished into 7 morphotype classes and 2 dominant coral genera: tabular *Acropora*, branching *Acropora*, massive *Porites*, branching, massive,

columnar, encrusting, foliose, and free-living. The classification of benthic groups was based on the NOAA Coral Reef Information System (NOAA 2014) and the 2022 edition of the Indo-Pacific Coral Finder (Kelley 2022).

4.2.3 Coral carbonate production

Coral carbonate production was estimated using two different methods:

a) The CoralNet methodology

Carbonate production rates of live coral cover in each photoquadrat were estimated using the *CoralNet* calcification tool (Courtney et al. 2021). This tool multiplies the percent cover of each labelled coral with an area-normalized calcification rate for each coral genus and morphotype. The calculation of area-normalized calcification rates is based on average Indo-Pacific calcification rates from the *ReefBudget* methodology (Perry et al. 2018) and adopted for use with planar imagery by accounting for median colony size, rugosity, and colony morphology (Courtney et al. 2021).

Area-normalized taxa-specific calcification rates are iteratively calculated as the 50^{th} percentile of a Monte-Carlo simulation (n = 10,000) using randomly selected values within the range of uncertainties of each taxon:

$$G = (n*cf*((c+b)*s*r+i))/10$$

where: $G = kg \ CaCO3 \ m^{-2} \ yr^{-1}$, $n = number \ of \ colonies \ per \ linear \ meter \ (\pm 95\%)$, $cf = conversion \ factor \ accounting \ for \ open \ space \ in \ branching \ morphologies \ (\pm \ uncertainty, Doszpot \ et \ al., 2019), <math>c = calcification \ rate \ coefficient \ (\pm \ uncertainties, \ Perry \ et \ al., 2018), b = microbioerosion \ rate \ coefficient, \ i = calcification \ rate \ intercept \ (\pm \ uncertainties, \ Perry \ et \ al., 2018), b = microbioerosion \ rate \ coefficient, \ i = calcification \ rate \ intercept \ (\pm \ uncertainties, \ Perry \ et \ al., 2018), s = median \ colony \ diameter, \ cm \ (\pm 95\%), \ r = \ rugosity \ (\pm \ uncertainty, \ González-Barrios \ and \ Álvarez-Filip, 2018), \ 10 = convert \ units \ to \ kg \ CaCO_3 \ m^{-2} \ yr^{-1}.$

b) The *ReefBudget* methodology

Coral carbonate production rates were also estimated using the Indo-Pacific *ReefBudget* methodology (Perry et al. 2018; Lange et al. 2022), after employing the Coral Colony Rugosity Index (CCRI) (Husband et al. 2022). First, the planar length of coral colonies in the surveyed photo quadrats were measured using the image analysis software JMicrovision (v1.3.4). Each

photo-quadrat was calibrated by drawing a 10 cm line along the gridlines of the photo-quadrats. After calibration, using the 1D measuring function, the planar length of every live coral colony along 3 horizontal lines (50 cm each) in each photo-quadrat, was measured (Figure 4.2:). This provided 1.5 m of survey line per photo-quadrat and a total of 15 m of survey line per transect (1.5 m x 10 photo-quadrats/transect). Each coral colony was identified to genus (a total of 37 genera were identified) and morphological levels (7 different morphotypes) (e.g., *Acropora* tabular, *Porites* massive, etc). Where a line fell on coral colonies that could not be identified to genus level due to partial visibility, corals were assigned a morphotype classification only (e.g. branching coral, massive coral).



Figure 4.2: Calibration and measurement of coral colony-size using 50 x 50 cm quadrat in J-Microvision. Photo-quadrat is calibrated using a 10cm line along the gridlines of quadrat. Planar length of live coral colonies, under 3 set horizontal lines (50 cm green lines) are measured using the 1D measuring function (red lines) on each photo-quadrat.

The planar length of each coral colony was then converted to its topographic contour length using appropriate taxa-specific rugosity values (R_{coral}) from the CCRI method (Husband et al. 2022):

Coral colony contour length = Colony planar length x Taxa-specific R_{coral} value

R_{coral} values from the CCRI method was derived by measuring 3172 individual coral colonies of 62 common Indo-Pacific hard coral genera-morphotypes from 3 different locations (Lizard Island, Heron Island, Great Barrier Reef as well as the London (United Kingdom) Natural History Museum's Indo-Pacific Dry Invertebrate collection) (see Husband et al., 2022 for details of method and datasets). The assumption is that the relationship between planar and contour length measurements of coral colonies is linear. Here, a Spearman's rank correlation test revealed a significant positive relationship between planar and contour lengths of all coral colonies (rho = 0.96, t = 206.16, df = 4858, p <0.001, Appendix C Figure S1).

To calculate total coral carbonate production rates, or Coral G (where $G = kg CaCO_3 m^{-2} yr^{-1}$), the contour length of each coral colony along with the genera-morphotype information was input into the Indo-Pacific *ReefBudget* coral carbonate spreadsheet (Perry et al., 2018; available at https:// geography.exeter.ac.uk/reefbudget/). In this study, the *ReefBudget* spreadsheet was modified to include local coral growth rates and skeletal densities to provide more accurate carbonate production estimates for the Chagos Archipelago (Lange et al. 2022). Coral growth rates were measured for 64 individual coral colonies from 22 dominant genera-morphotypes (Lange and Perry 2020), and skeletal densities assessed for 136 individual coral colonies from 35 genera-morphotypes collected from 8-10 m deep forereefs (Lange et al. 2022). Due to lack of depth-specific data, it was assumed that coral calcification rates were similar across both shallow and moderate depths.

To compare coral carbonate production rates from the two-census based methodologies, genera-level coral assemblage data from *ReefBudget* was grouped into 7 morphotypes and the two dominant genera: *Acropora* and *Porites* to match identification done in *CoralNet*.

4.2.4 Coral colony size structure

Coral colony sizes were extracted from the dataset to assess the variability in the size structure across depths and atolls. As described above, coral colony size was measured as planar length but converted to contour length using the Coral Colony Rugosity Index (CCRI) (Husband et al. 2022). Identified genera were grouped into: tabular *Acropora*, branching *Acropora* (mainly caespito-corymbose, digitate and few arborescent), massive *Porites*, branching (all taxa excluding *Acropora*), and massive (all other massive, submassive and columnar taxa), encrusting (all taxa), foliose (all taxa) and `other` (plating, frondose and free-living), following (Lange et al. 2022). A total of 4858 colony sizes were recorded across all morphotypes, depth, atolls, and sites.

4.2.5 Statistical analyses

4.2.5.1 Community composition

To assess whether benthic communities varied across depth and atolls, composition (using data from *CoralNet*) was visualised at two taxonomic levels: 1) proportional cover of benthic groups (hard coral, soft coral, sponge, turf, fleshy macroalgae, CCA, *Halimeda* spp., sand, rubble, reef pavement, dead coral, and `Other`) and, 2) hard coral assemblage (identified to genus level), using non-metric multidimensional scaling (nMDS: vegan package, Oksanen, 2015) based on Bray-Curtis dissimilarity matrices on square-root transformed data. The nMDS were computed on 3 dimensions (k = 3) with ordination stress values < 0.2, which was evaluated with a scree plot. Envfit analyses were performed to identify 1) benthic groups and 2) coral taxa that significantly contributed to average dissimilarity among sites and across depth (envfit: vegan package). The strength of the association of 1) benthic groups and 2) coral taxa to the ordination was determined by permutation-based p-values using 9999 permutations.

To examine differences in benthic community composition across depths and atolls, two-way nested permutational multivariate analyses of variance (PERMANOVA; Anderson, 2017) were performed on: 1) benthic groups, and 2) hard coral assemblage as a function of the interaction between depth (2 levels, fixed factor) and atolls (4 levels, fixed factor), with site (random factor) nested in atoll (using 9999 permutations; adonis2: vegan package). Where a significant interaction between depth and atoll was found, further within-atoll analyses were carried out to identify the depth-dependent effects at each atoll, using one-way nested PERMANOVAs. Where benthic groups and hard coral assemblage varied significantly among atolls, pairwise tests were used to compare differences among atolls (using 9999 permutations, permanova_pairwise: ecole package, Smith, 2021). Multivariate homogeneity tests (betadisper: vegan package) indicated similar dispersion means for hard coral assemblage among atolls but were slightly higher at deeper reefs compared to shallow reefs (Table 4.1).

In addition, indicator taxa analyses were conducted to identify combinations of coral taxa that significantly associate with shallow and deep reefs across each atoll. The joint occurrences of two or more coral genera with depth and atolls can be used as a proxy of the biotic and abiotic factors of the location at which they occur (Cáceres and Legendre 2009). Hard coral assemblage data was converted into presence/absence data and indicator taxa were identified using a specificity (A_t) and sensitivity (B_t) threshold of 0.4-0.6 and 0.25, respectively. Significance was assessed using PERMANOVA with 9999 permutations (indicators: indicators: package, Cáceres, 2020).

4.2.5.2 Coral cover and carbonate production

To assess the difference in proportional coral cover across depth and atoll, and to compare carbonate production estimates of the two methods, we ran linear hierarchical models within a Bayesian framework (brm: brms package, Bürkner, 2018). Total coral cover (response variable modelled as a function of an interaction between depth and atoll) and coral carbonate production (response variable modelled as a function of an interaction between depth, atoll, and method) were examined with a gaussian distribution (population-level effects). Site (group-level effects) was nested in atoll to control for the natural variation in proportional coral cover and coral carbonate production between sites. Models were fitted with 2000 iterations across 4 chains, using the Markov Chain Monte Carlo (MCMC) algorithm and weakly informative priors on the regression parameters in the model (Appendix C Table S2). All posterior samples were extracted from 4000 draws to simulate the response variables. Posterior distributions were assessed using Gelman-Ruban convergence R-hat values of <1.05 and a minimum effective sample size (ESS) of > 1000 for all parameters (Gelman et al., 2013). Posterior predictive checks were used to assess model fits (bayesplot package, Gabry and Mahr, 2017 and tidybayes package Kay, 2022). The influence of each predictor (depth, atoll, and method) on total coral carbonate budget and proportional coral cover was assessed using average marginal effects (emmeans: emmeans package, Lenth, 2022). Uncertainty related to the models' posterior estimates (median) was interpreted with 65% and 95% credible intervals. Strong and weak evidence of an effect was interpreted when 95% and 65% of the intervals did not intercept zero, respectively (Robinson et al. 2019a; González-Barrios et al. 2021).

The effect of depth on the proportional contribution of different coral morphotypes to total carbonate production was examined using a set of generalised linear mixed-effects models (GLMMs). GLMMs, fitted with a beta distribution and logit-link function, and zero-inflation extensions when proportional data were over-dispersed and zero-inflated (glmmTMB: glmmTMB package, Brooks et al., 2017), were used to model the difference in proportional contribution of six coral morphotypes (tabular *Acropora*, branching *Acropora*, massive *Porites*, branching, massive, encrusting/foliose) across depth (fixed factor: 2 levels), atolls (fixed factor: 4 levels) and methods (fixed factor: 2 levels). Site (random effect) was nested in atoll to constrain natural variation across transects at site level. Assumptions of normality and homoskedasticity were visually assessed using residual plots (plotQQunif, plotResiduals, testDispersion: DHARMa package, Hartig, 2022). Where a zero-inflated model was used, a

zero-inflation test was carried out to verify the expected distribution of zeros under the fitted model against observed values (testZeroInflation: DHARMa package, Hartig, 2022). Rarely occurring morphotypes such as free-living, plating, and frondose were not included in the analyses.

4.2.5.3 Coral colony size structure

Size-frequency distributions and size-class abundance across depths and atolls were plotted to visualise the difference in colony size structure for: 1) all colonies and 2) each morphotype. Following statistical analyses in Dietzel et al (2020) and Lange et al (2022), general linear mixed effect models (lmer:lmerTest package, Kuznetsova et al., 2017) were run to assess the difference in mean size and standard deviation (SD) of all colonies and skewness of size-frequency distribution across depth and atolls. Homogeneity of variance and normality checks were performed using Shapiro-Wilk and Levene tests and visualised using residual plots. Size-class abundance were obtained for log-transformed colony size data, which were binned into small (first quintile), medium (second-fourth quintile) and large (fifth quintile) colonies. Using bootstrap resampling (n = 1000), uncertainties in the difference in size-class abundance between shallow and deep reefs: 1) all colonies and 2) each morphotype were assessed. The relative percentage difference in size-class abundance between shallow and moderate depths was calculated as follows:

$\frac{No \ of \ colonies \ at \ moderate \ depth - No \ of \ colonies \ at \ shallow \ depth}{No \ of \ colonies \ at \ shallow \ depth} \ x \ 100$

All statistical analyses were carried out in R 4.1.1 (R Development Core Team 2021). Data were visually assessed using tidyverse package (Wickham et al. 2019).

4.3 Results

4.3.1 Benthic community composition

Benthic community composition showed significant depth-by-atoll interaction (PERMANOVA, depth*atoll: Pseudo $F_{3, 95} = 2.28$, p = < 0.001), indicating that the difference in benthic communities with depth varied among atolls (Figure 4.3). Within-atoll analyses

revealed significant variation in benthic community composition between shallow and moderate reefs in each of the four atolls (PERMANOVA, EG, SA, PB: p < 0.001 and GCB: p = 0.004, Table 4.1, Appendix C Figure S2).



Figure 4.3: Non-metric multi-dimensional scaling (nMDS) plots of a) benthic groups and b) hard coral assemblage from 16 sites in the Chagos Archipelago, showing clustering of communities across depth: shallow (10 m) and deep (17.5 m) reefs, based on Bray-Curtis

dissimilarities of square-root transformed data. Ellipses represent dispersion of shallow (yellow) and deep (blue) communities from community centroids at 95% confidence interval – symbols indicate surveyed atolls – Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Overlaid (a) benthic groups (envfit analysis) and (b) coral taxa (indicator taxa analysis) represent taxonomic groups that significantly contributed to the ordination.

Table 4.1: Variation in benthic community using permutational analysis of variance (PERMANOVA) and dispersions tests between shallow and moderate reefs across and within atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Pairwise comparisons among atolls are provided in Appendix C Table S2.

a) Benthic groups	PERMANOVA	Dispersion test
Atoll*Depth	Pseudo- $f_{3,95} = 2.28$ p<0.001	Pseudo- $f_{7, 88} = 1.03$ p=0.411
Within-atoll variation		
Egmont	Pseudo- $f_{1, 23} = 5.87$ p < 0.001	Pseudo- $f_{1, 22} = 0.41$ p = 0.53
Great Chagos Bank	Pseudo- $f_{1, 23} = 3.26$ p = 0.004	Pseudo- $f_{1, 22} = 0.01$ p = 0.96
Peros Banhos	Pseudo- $f_{1, 23} = 6.86$ p < 0.001	Pseudo- $f_{1, 22} = 0.48$ p = 0.49
Salomon	Pseudo- $f_{1, 23} = 6.36$ p < 0.001	Pseudo- $f_{1, 22} = 2.92$ p = 0.09

Hard coral assemblages showed independent significant effects of depth and atoll (PERMANOVA, depth: Pseudo $F_{1,95} = 9.04$, p = < 0.001, atoll: Pseudo $F_{3,95} = 3.29$, p = < 0.001, depth*atoll: Pseudo $F_{3,95} = 1.04$, p = 0.174, Table 4.2). Pairwise comparisons indicated the hard coral assemblage at Egmont was significantly different to those at sites in the Great Chagos Bank, Peros Banhos and Salomon, and the hard coral community at Great Chagos Bank was significantly different to Salomon (Appendix C Table S3). Indicator taxa analysis found a total of 9 coral genera as well as the `Other` category that characterised the hard coral community across depths and atolls. Joint occurrences of *Pocillopora, Acropora* and *Porites*, *Montipora, Goniastrea, Favites, Platygyra, Psammocora, Pavona* and `Other` hard corals were significantly associated with moderate depth at 17.5 m. Genera characterising each atoll are provided in Appendix C Table S4.

Table 4.2: Variation in hard coral assemblage using permutational analysis of variance (PERMANOVA) and dispersions tests between shallow and moderate reefs across and within atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Pairwise comparisons among atolls are provided in Appendix C Table S2.

Hard coral assemblage	PERMANOVA	Dispersion test	
Depth*Atoll	Pseudo- $f_{3,95} = 1.04$		
	p = 0.174	-	
Denth	Pseudo- $f_{1,95} = 9.04$	Pseudo- $f_{1, 94} = 4.222$	
Depth	p<0.001	p = 0.043	
A toll	Pseudo- $f_{3,95} = 3.28$	Pseudo- $f_{3,92} = 0.646$	
Atom	p<0.001	p = 0.587	

4.3.2 Coral cover and carbonate production

Total hard coral cover ranged from $9.5 \pm 0.5\%$ to $28.8 \pm 1.4\%$ and was consistently higher on shallow ($22.6 \pm 1.1\%$) than at moderate depth ($16.3 \pm 0.8\%$) (Figure 4.4, Table 4.3). There was significant variation in total hard coral cover among atolls. Both Egmont and Salomon showed higher hard coral cover at both depths compared to Peros Banhos and Great Chagos Bank (Figure 4.4, Table 4.3).



Figure 4.4: a) Predicted coral cover between shallow (10 m) and moderate (17.5 m) depths and b) posterior distributions of standardised effects of depth on variation in coral cover at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points in (b) indicate median estimates and bars represent 65% and 95% credible intervals. Strong and weak

effects of depth are interpreted when 95% and 65% of the intervals do not intercept zero, respectively.

Table 4.3: Predicted coral cover (mean \pm SE) between shallow (10 m) and moderate (17.5 m) reefs with average standardised effects of depth on variation in coral cover across atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Strong and weak effects of depth are interpreted when 95% and 65% of the credible intervals (CI) do not intercept zero, respectively.

		Coral cover				65% CI		95% CI	
Atoll	Depth	Maar		се Се	Effects	Lower		Lower	
		Mean	ΙΞ	SE		CI	Upper CI	CI	Upper CI
	10m	28.75	±	1.41	3.33	3.25	3.43	3.14	3.51
EG	17.5m	20.75	±	1.02	3.01	2.92	3.10	2.81	3.19
	10m	13.18	±	0.72	2.54	2.43	2.64	2.33	2.78
GCB	17.5m	9.50	±	0.52	2.22	2.11	2.31	2.00	2.43
	10m	21.83	±	1.88	3.02	2.92	3.12	2.83	3.23
PB	17.5m	15.78	±	1.36	2.70	2.59	2.79	2.50	2.92
	10m	26.63	±	1.35	3.25	3.17	3.36	3.06	3.46
SA	17.5m	19.25	±	0.97	2.93	2.82	3.01	2.71	3.13

Similar trends were observed in coral carbonate production rates across depths, where mean coral carbonate production on shallow reefs was higher $(4.8 \pm 0.3 \text{ G})$ than at moderate depth $(3.1 \pm 0.2 \text{ G})$ for all atolls, except at Great Chagos Bank where no variation was observed between shallow and moderate depths as indicated by the overlap in posterior distributions of all samples (Figure 4.5, Table 4.4). There were significant differences in coral carbonate production rates derived from both methods, with *CoralNet* estimates lower than *ReefBudget* estimates across both depths and all atolls except in Great Chagos Bank, where coral carbonate production was relatively low at both shallow and moderate depths (Figure 4.5, Table 4.4).



Figure 4.5: a) Predicted coral carbonate production between shallow (10 m) and moderate (17.5 m) reefs and b) posterior distributions of standardised effects of depth on variation in coral carbonate production at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) between *CoralNet* (CN) and *ReefBudget* (RB). Points in (b) indicate median estimates and bars represent 65% and 95% credible intervals. Strong and weak effects of depth are interpreted when 95% and 65% of the credible intervals (CI) do not intercept zero, respectively.

This underestimation of coral carbonate production rates was equivalent to 1.71 ± 0.19 G (mean \pm SE). It was found that the difference between *ReefBudget* and *CoralNet* was smaller for lower values of coral carbonate production rates and increased as coral carbonate production rates become larger (Figure 4.6).



Figure 4.6: Regression between transect level coral carbonate production rates (Coral G measured in kg CaCO₃ m⁻² yr⁻¹) from *CoralNet* against rates from *ReefBudget* (solid blue line with a correlation, r^2 of 0.86). The dashed line represents the identify line (y=x) and indicate where values should fall if both methods yield the same production rates.

Table 4.4: Predicted coral carbonate budget (mean \pm SE) between shallow (10 m) and moderate (17.5 m) reefs with average standardised effects of depth on variation in coral carbonate budget across atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Strong and weak effects of depth are interpreted when 95% and 65% of the credible intervals (CI) do not intercept zero, respectively.

Atoll Depth			Coral G			65% CI		95% CI		
		Method Mean ± S		SE	Effects	Lower CI	Upper CI	Lower CI	Upper CI	
	10m	CoralNet	5.40	±	0.30	1.66	1.57	1.76	1.45	1.86
EC	10111	ReefBudget	7.32	±	0.41	1.96	1.86	2.06	1.74	2.15
EU	17.5m	CoralNet	2.78	±	0.18	0.98	0.88	1.09	0.75	1.20
17.5m	ReefBudget	4.21	\pm	0.28	1.40	1.31	1.52	1.17	1.62	
	GCB 17.5m	CoralNet	1.56	±	0.17	0.36	0.28	0.48	0.15	0.58
CCR		ReefBudget	2.45	±	0.27	0.82	0.73	0.93	0.59	1.02
UCD		CoralNet	1.78	±	0.25	0.46	0.37	0.56	0.25	0.67
17.311	ReefBudget	2.55	±	0.36	0.82	0.72	0.91	0.61	1.03	
	10	CoralNet	3.59	±	0.32	1.23	1.14	1.34	1.03	1.45
DD	10111	ReefBudget	5.45	±	0.49	1.64	1.54	1.74	1.43	1.86
T D	rD	CoralNet	2.01	±	0.26	0.55	0.43	0.65	0.31	0.79
17.311	ReefBudget	3.84	±	0.49	1.19	1.08	1.32	0.94	1.46	
10m	CoralNet	4.83	±	0.53	1.49	1.40	1.60	1.27	1.69	
	10111	ReefBudget	7.95	±	0.86	1.99	1.89	2.09	1.78	2.20
SA	17.5m	CoralNet	2.69	±	0.40	0.84	0.72	0.94	0.63	1.08
17.5m	ReefBudget	4.98	±	0.74	1.46	1.34	1.56	1.22	1.69	

4.3.3 Contribution of coral morphotypes to total coral carbonate production

There was significant variation in the contribution of different coral morphotypes to coral carbonate production between shallow and moderate depths and between methods (Figure 4.7, Appendix C Table S5). Shallow reefs had higher contributions by branching *Acropora* (shallow: 24.0 ± 2.1%; moderate: 15.2 ± 1.8%, depth: χ^2 (1,168) = 12.278, p < 0.001) and massive *Porites* (shallow: 21.5 ± 1.7%; moderate: 18.6 ± 1.4%, depth: χ^2 (1,165) = 8.589, p = 0.003). Encrusting and foliose corals contributed more at moderate depth (shallow: 18.2 ± 1.4%; moderate: 31.3 ± 1.6%, depth: χ^2 (1,174) = 12.278, p < 0.001). Tabular *Acropora* contributed to a relatively small proportion of the total carbonate production, which was higher on shallow reefs (shallow: 9.6 ± 1.6%; moderate: 3.2 ± 0.7%, depth: χ^2 (1,168) = 4.868, p = 0.027). There was no significant difference in carbonate production by branching (shallow: 9.5 ± 1.2%; moderate: 6.9 ± 1.2%, depth: χ^2 (1,165) = 2.755, p = 0.096) and massive corals (shallow: 7.8 ± 1.0%; moderate: 11.7 ± 1.2%, depth: χ^2 (1,165) = 0.585, p = 0.444) between depths.



Figure 4.7: Contribution of coral morphotypes to coral carbonate production (coral G) between shallow (10 m) and moderate (17.5 m) reefs between *CoralNet* and *ReefBudget* at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

Depth effects furthermore showed significant variation among atolls (Figure 4.7, Appendix C Table S5). Tabular *Acropora* contributed more to the carbonate production at shallow (25.1 \pm 4.6%) compared to moderate depth (9.4 \pm 2.4%) at Salomon (Tukey, t(168) = 5.989, p < 0.001), but not at other atolls. The contribution of massive *Porites* to carbonate production was significantly higher at shallow reefs at Egmont (shallow: 27.6 \pm 4.7%; moderate: 15.7 \pm 2.9%, Tukey, t(165) = 3.759, p = 0.006). The contribution of encrusting/foliose corals to carbonate production was higher at moderately deep reefs at all atolls (EG: shallow: 11.3 \pm 1.5%; moderate: 33.5 \pm 3.8%, Tukey t(174) = -7.115, p < 0.001, PB: shallow: 16.6 \pm 2.4%; moderate: 29.0 \pm 2.8%, t(174) = -4.265, p < 0.001, SA: shallow: 19.6 \pm 2.2%; moderate: 31.2 \pm 3.0%, t(174) = -3.782, p = 0.005), except at Great Chagos Bank (shallow: 25.3 \pm 3.6%; moderate: 31.2 \pm 3.4%, Tukey, t(174) = -1.953, p = 0.516).

Branching *Acropora* and massive corals showed significant atoll-dependent variation in carbonate production (Figure 4.7, Appendix C Table S5). Pairwise comparisons indicated Egmont showed higher contribution from branching Acropora compared to Great Chagos Bank. In contrast, Great Chagos Bank had higher contribution of massive coral cover compared to Egmont (Tukey, t(165) = -2.978, p = 0.017), Peros Banhos (Tukey, t(165) = 3.101, p = 0.012), and Salomon (Tukey, t(165) = 3.886, p < 0.001).

Comparing the two methods, significant differences were observed in the contribution of massive corals (Figure 4.7, Appendix C Table S5, depth x method: $\chi^2(1,165) = 7.621$, p = 0.006). Compared to *ReefBudget, CoralNet* showed higher contributions of massive corals to carbonate production at both shallow (*CoralNet*: 13.0 ± 1.5%; *ReefBudget*: 2.5 ± 0.6%; Tukey, t(165) = 6.781, p < 0.001) and moderate depths (*CoralNet*: 15.5 ± 1.90%; *ReefBudget*: 7.8 ± 1.2%; Tukey, t(165) = 4.758, p < 0.001). There was no difference in the contribution by other morphotypes.

4.3.4 Coral colony size structure

Significant variation in coral population size structures was recorded between depths and among atolls. A total of 2485 and 2373 coral colonies were recorded at shallow and moderate depths, respectively, with a higher mean coral colony size at 10 m (14.7 ± 0.4 cm) than at 17.5 m (10.6 ± 0.3 cm) (Figure 4.8, Appendix C Table S6, GLMM: atoll x depth: F(3,12) = 9.41, p = 0.001). The standard deviation (SD) of colony size also significantly declined with increasing depth (except at GCB, Figure 4.8, Appendix C Table S6, GLMM: atoll x depth: F(3,12) = 3.82, p = 0.039), indicating a less varied colony size structure at moderate depth compared to shallow reefs. This difference in coral population structure between depths was most pronounced at Egmont (Appendix C Table S6, Tukey: mean colony size - t(12) = 7.79, p < 0.001; SD - t(12) = 4.17, p = 0.001) and Salomon (Appendix C Table S6, Tukey: mean colony size - t(12) = 4.49, p < 0.001; SD - t(12) = 3.01, p = 0.011). Overall coral colony size distributions were positively skewed and showed higher positive values on shallow reefs independent of atoll (Figure 4.8, Appendix C Table S6, GLMM: depth: F(1,12) = 7.70, p = 0.017), suggesting that the shallow reefs of all atolls had a higher occurrence of medium and large colonies compared to moderate depth.



Figure 4.8: a) Size-frequency distributions of all coral colonies between shallow (10 m) and moderate (17.5 m) reefs at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA); b) change in the abundances of small (derived from first quintile), medium (derived from second-fourth quintile), and large (derived from fifth quintile) coral colonies with increasing depth and c) variation in mean colony size, standard deviation in coral colony size and skewness of size distributions of all coral colonies between depth among atolls. A positive change in size-class abundances indicate higher abundances with increasing depth, i.e., on moderate reefs at 17.5 m relative to shallow reefs at 10 m.

However, comparisons of taxa-specific size class distributions showed significant variation among both depths and atolls (Figure 4.9, Figure 4.10, Appendix C Table S7). Coral colonies on shallow reefs showed higher abundance of tabular *Acropora*, branching *Acropora* and massive *Porites* of all size classes, as well as large branching corals, which varied among the four atolls (Figure 4.9, Figure 4.10). Abundance of all size classes of encrusting/foliose corals were higher at moderate depths, especially at Egmont and Salomon (Figure 4.9, Figure 4.10). Higher occurrence of medium and large-sized massive corals was also found at moderate depth at Egmont and Great Chagos Bank (Figure 4.9, Figure 4.10). Medium-sized branching corals were more abundant at moderate depth at Great Chagos Bank (Figure 4.9, Figure 4.10).



Figure 4.9: Size-frequency distributions of coral morphotypes between shallow (10 m) and moderate (17.5 m) reefs at atolls: Egmont, Great Chagos Bank, Peros Banhos and Salomon.



Figure 4.10: Change in abundance of coral morphotypes colonies with increasing depth, separated in size-class (small colonies: first quintile, medium colonies: second-fourth quintile, and large colonies: fifth quintile). Positive % change indicate higher abundance of coral colonies at moderate depth (17.5 m) and negative % change indicate higher coral colony abundance at shallow depth (10 m). A strong and a weak % change in colony abundances between depth were interpreted when 95% and 66% confidence intervals did not intercept zero, respectively.

4.4 Discussion

Our understanding of reef framework production across depth gradients on contemporary reefs is very limited (Perry and Alvarez-Filip 2018, Lange et al 2020) Here we show significant depth variation in in benthic community composition, coral cover, and carbonate production rates, which varied across the remote reefs of the Chagos Archipelago . Whilst the atoll-scale variation is consistent with existing evidence of spatial variation in coral carbonate production among different sites, reef habitats and across wider seascape at depths ≤ 10 m (Van Woesik and Cacciapaglia 2018; Lange et al. 2020), our results highlight the vertical zonation of coral carbonate production rates within shallow-water reefs (< 30 m). We show higher community level carbonate production rates by corals on shallow reefs (10 m) compared to moderate depths (17.5 m).

Our findings are comparable to two early studies that surveyed large depth gradients (10-60 m: Land 1979; 10-30 m: Heiss 1995), and recent studies, which showed decreasing net carbonate production rates with depth, even within the very shallow reef zones (0-10 m) (Brown et al. 2021; Davis et al. 2021; Divan Patel et al. 2023). The decline in coral carbonate production with increasing depth reflects the natural variation in biophysical factors across depth. Two major factors that affect community composition and calcification rates, and therefore total carbonate production, are light and temperature (Baker and Weber 1975; Venti et al. 2014; Kahng et al. 2023), both of which naturally decrease with increasing depth (Kahng et al. 2019). Differences in carbonate production rates among atolls furthermore suggest sitespecific variation in abiotic environmental controls (Silbiger et al. 2017; Ross et al. 2022). Carbonate production rates at shallow reefs were highest at Egmont and Salomon atoll (> 7.0G), causing large depth differences at these atolls, whilst rates at Great Chagos Bank are very low (< 2.6G) across both depths. Variation in large scale hydrodynamic forcings such as internal wave and upwelling activities, which import allochthonous food subsidies onto shallow reef systems that promotes heterotrophy and coral growth, can cause an increase in total alkalinity and dissolved inorganic carbon which positively influence coral calcification rates (Rodriguez-Ruano et al. 2023; Gómez et al. 2023). Other environmental factors such as reef slope (Sheppard 1982) and wave exposure regime can also structure coral communities and carbonate production rates among sites (Falter et al. 2013; Caballero-Aragón et al. 2023). Such hydrodynamic settings may occur around Egmont and Salomon, favouring higher abundances of Acropora (tabular and branching), which promote higher overall carbonate production rates compared to the other atolls (Robinson et al. 2023; Harris et al. 2023).

Community level variation in carbonate production rates can be driven by relative abundances of different coral morphotypes (Alvarez-Filip et al. 2013; Cabral-Tena et al. 2018) and demography of coral populations, i.e., coral colony sizes (Vermeij and Bak 2003). As coral species interact with different environmental gradients across depth, they build community assemblages with different morphotypes and growth characteristics, and can adapt their individual tissue thickness, linear extension, calcification rates, skeletal density and colony size (Bosscher 1993). Higher coral carbonate production rates on shallow reefs in this study reflect higher abundances of medium and large colonies compared to moderate depths populated with a relatively higher number of small colonies (Bak and Nieuwland 1995; Kramer et al. 2020). Characteristic of shallow water environments, observed branching and tabular morphotypes show higher photosynthetic rates in environments with higher irradiance levels and water circulation (Tamir et al. 2019), which can lead to higher growth rates and greater contributions to carbonate production compared to conspecifics growing deeper (Edmunds and Burgess 2017; Carlot et al. 2022; Tortolero-Langarica et al. 2022). In contrast, by slowly extending their planar surface area to increase light capture at depth, encrusting and foliose corals on deeper reefs tend to build thinner skeletons and accrete less carbonate per unit area compared to shallow water counterparts (Cabral-Tena et al. 2018; Kahng et al. 2023). These depth-related differences in calcification are not reflected in the present study, as the only available growth rates are from <10 m depths. Depth differences in carbonate production rates are therefore conservative estimates and are likely even higher than presented here.

Both *ReefBudget* and *CoralNet* employ a census-based approach i.e., they quantify the size or cover of coral colonies and multiply by calcification rates from the Chagos Archipelago or the Indo-Pacific region, respectively (Courtney et al. 2021; Lange et al. 2022). The *ReefBudget* method employs growth rates from the Chagos Archipelago, that are mostly lower than Indo-Pacific averages (Lange et al. 2022). However, method comparisons showed significantly higher coral carbonate production rates from *ReefBudget* at both shallow and moderate depths. Underlying the *ReefBudget* method in this study is a digitised line-intercept technique (1.5 m/0.25 m² photo-quadrat) compared to a randomised stratified point count method (15 points/0.25 m² photo-quadrat) employed in *CoralNet*. Previous comparisons between digitised line-intercept transects and point-count methods from the Western Indian Ocean region showed no significant difference in benthic community cover between the two techniques (Urbina-Barreto et al. 2021). The consistent difference between the two methodologies could thus be linked to the techniques that are used to quantify carbonate production rates in *CoralNet* and *ReefBudget*. *ReefBudget* provides more realistic colony size-based calculations which likely

explain higher calcification rates compared to area-normalised scaling and Monte-Carlo simulations of the colony size estimates in *CoralNet* (Courtney et al. 2021). Additionally, current carbonate measurements in *CoralNet* include micro/macro-bioerosion rates within coral calcification rates, which could result in lower production rates than *ReefBudget* (Courtney et al. 2021).

Past disturbance history can provide insights into coral carbonate production differences (Brown et al. 2021; Lange et al. 2022). The most recent major disturbance event in the Chagos Archipelago was the third global warming event in 2015–2017 that caused a 77% reduction in mean coral carbonate production on shallow reefs (8–10 m) (Lange and Perry 2019). Similar patterns of declining carbonate budget states due to widespread coral bleaching were reported at shallow depths (2-10 m) of the Indian Ocean region in the Maldives (Perry and Morgan 2017b) and Seychelles (Januchowski-Hartley et al. 2017), as well as the wider Pacific (Cabral-Tena et al. 2018; Courtney et al. 2022) and Caribbean (Perry et al. 2013; Manzello et al. 2018; Estrada-Saldívar et al. 2019; Molina-Hernández et al. 2020). However, the change in coral community level carbonate production due to thermal stress events below 10 m depth remains unknown. Growing evidence of coral bleaching and mortality across larger depth gradients within both shallow-water (2–27 m) and mesophotic (>30 m) reefs due to severe warming events (Sheppard et al. 2017; Muir et al. 2017; Morais and Santos 2018; Frade et al. 2018; Baird et al. 2018; Crosbie et al. 2019; Venegas et al. 2019) further highlights the importance of examining changes in carbonate production rates across depths on shallow reef systems (Perry and Alvarez-Filip 2019; Lange et al. 2020).

Recent findings spanning multiple depth gradients across the forereefs of the Chagos Archipelago (5–25 m) show distinct depth-related changes in coral cover and population structure following recurring thermal stress: 1) a greater decline in coral cover at shallower depth (5–10 m) compared to deeper reefs (10–25 m) (Chapter 3); 2) a decline in competitive species such as tabular and branching *Acropora* and *Pocillopora* and a higher persistence of stress tolerant taxa with encrusting and foliose morphologies, and 3) faster recovery of Acroporids and encrusting genera at shallower reefs compared to deeper sites (Sheppard et al. 2008, 2013b, 2017, 2020; Lange et al. 2022). In line with carbonate budget surveys in 2021 (Lange et al. 2022) and previous recovery trends across depth (Sheppard et al. 2008, 2013b, 2017, 2020), higher coral carbonate production rates observed on shallow reefs may partly be driven by environmental conditions, such as light and temperature, that promote faster recovery

of fast-growing, high carbonate producing taxa compared to slow growing and low framework building taxa that thrive at lower temperature and irradiance levels on deeper reefs.

Surviving coral populations are key to recovery trajectories of coral reef assemblages and their contribution to net carbonate budgets (Dietzel et al. 2020; Lange et al. 2022). Disproportionate loss of susceptible key reef-building taxa resulting in low coral recruitment densities and large die-offs of small vulnerable colonies due to repeated intense bleaching events can result in increased homogenisation of coral communities (Bruckner and Hill 2009; Gilmour et al. 2022; Ford et al. 2023), and a subsequent decline in coral carbonate production across both shallow and deeper reefs (Perry and Alvarez-Filip 2019; Lange and Perry 2019; Estrada-Saldívar et al. 2019; Molina-Hernández et al. 2020). However, our results indicate the presence of all size classes (small, medium, and large colonies) within morphotypes at shallow and moderate depths, suggesting a positive recovery trajectory of reefs and coral carbonate production in coral carbonate production among atolls also highlights different recovery speeds among sites (Lange et al. 2022).

Our results capture coral carbonate rates 6–7 years after the third global bleaching event, which is within the timeframe (7-12 years) that coral assemblages typically recover and reassemble towards pre-disturbance coral dominated levels in the absence of further disturbance events (Johns et al. 2014; Gouezo et al. 2019). Whilst the historical and on-going recovery of coral carbonate productivity may be linked to the lack of direct anthropogenic impacts across the uninhabited atolls of the Chagos Archipelago, slower recovery of branching and tabular corals at one of the four atolls (i.e., in Great Chagos Bank) suggests that bleaching can cause homogenisation of carbonate production across depth. Furthermore, the significant decrease and possible permanent loss of key carbonate producing species such as Isopora palifera raise concerns about unpredicted shifts in coral communities due to repeated bleaching events (Sheppard et al. 2020). It is likely that increasingly small recovery windows due to the projected increase in frequent and severe bleaching events may, in the long term, supress primary framework production rates and compromise reefs' ability to support reef framework accretion across depths (De'Ath et al. 2012; Perry and Alvarez-Filip 2019; Cheung et al. 2021). By assessing depth-dependent changes in coral carbonate productivity in a recovering remote reef system, this study provides a basis to quantify the magnitude and extent of depth changes in carbonate producing processes at increasingly homogenised reefs across the wider Indo-Pacific.

5.1 Key findings

It is becoming increasingly evident that recurrent disturbance events are globally transforming coral reef assemblages across multiple spatial and temporal scales (Cresswell et al. 2023). Elucidating the spatial variation in benthic community composition and ecological function across depth gradients of contemporary shallow coral reefs (0-30 m) is therefore key to understanding how coral reef communities reorganise vertically; whilst providing the ability to predict future coral reef trajectories and to better manage them. This thesis examined the depth variation in benthic communities and geo-ecological functions of coral assemblages within a remote shallow reef system (5-25 m). The aims of this research were to:

i) Assess variation in depth zonation in benthic communities within and among contemporary reef systems

Using benthic community data 15 years following the 1998 massive bleaching event, **Chapter 2** assessed differences in benthic communities (broad benthic groups and coral assemblages) between shallow (5–10 m) and deep (20–25 m) reef zones, when the reefs were approaching full recovery. Whilst within-atoll comparisons showed clear depth-dependent variation in benthic communities and coral assemblages, significant depth-by-atoll variation was observed suggesting the difference in benthic communities and coral assemblages between shallow and deep reefs varied among atolls. Among all atolls, shallow reef zones consistently showed higher live and dead coral cover compared to deep zones, whilst significant variability was observed in other benthic groups such as CCA, sponge, turf, macroalgae and soft coral. At the coral assemblage level, the two depth generalists *Acropora* and *Porites* were found at both depths at all atolls.

ii) Assess the response of benthic communities across depths to recurring thermal stress

In Chapter 3, I examined how benthic communities responded to the 2015–2017 back-to-back bleaching events across multiple depth gradients (i.e., four depth ranges: 5–10m, 10–15 m, 15–20m, 20–25 m). Significant differences that varied across depth zones were observed in benthic communities before (2013/2014) and after (2018/2019) the successive warming events. By calculating the change in benthic groups before and after the recurring bleaching events, greater changes in benthic groups were observed at shallow (5–15 m) reef zones than at deeper reefs

zones (15–25 m). By examining the difference between initial and repeated thermal stress, it was found that benthic groups showed variable response to thermal stress across depth. For instance, initial thermal stress was associated with hard coral cover loss compared to soft coral loss which was better predicted by cumulative heat stress following the recurring bleaching events.

iii) Assess how important reef function such as coral carbonate production vary across depth?

Finally, in Chapter 4, carbonate production rates of coral assemblages were assessed at shallow (10 m) and moderate (17.5 m) depths. Using a census-based approach on digitised photoquadrats, and examining coral colony sizes and morphotypes, higher carbonate productivity was found at shallow reef zones compared to moderate depths. High coral carbonate production rates at shallow depths followed higher abundance of medium and large colonies (of all morphotypes) and dominated by fast-growing high framework building Acroporids and weedy massive *Porites*. Comparatively, deeper reef zones, characterised by low relief encrusting and foliose morphotypes showed lower carbonate productivity. By collecting coral morphotypes and colony size data 6–7 years following the 2015–2017 repeated warming events, the results in this chapter indicate positive on-going recovery of the coral assemblage and carbonate productivity across both shallow and moderate depths.

A first comparison between two census-based methodologies was carried out and revealed higher coral carbonate production estimates from *ReefBudget* compared to *CoralNet*. Despite both methods utilising similar carbonate production rates, it was evident that coral colony size measurements from *ReefBudget* provided a more realistic estimate of coral carbonate productivity compared to Monte-Carlo simulation of colony sizes and area-normalised scaling in *CoralNet*.

5.2 Implications for present and future coral reefs

This research indicates strong atoll-dependent depth zonation patterns and heterogeneity of benthic assemblages. By surveying multiple depth gradients, this study shows distinct zonation patterns exist within locations, but variable distribution of contemporary benthic communities and coral assemblages across depths were found among locations (**Chapter 2, Chapter 3**). Contrary to depth-dependent zonation expectations elucidated decades ago (Sheppard 1982; Done 1983) and in keeping with recent observations from contemporary coral reefs

communities (Muir et al. 2017; Giraldo-Ospina et al. 2020; Richardson et al. 2023), significant depth-by-atoll interactions indicate that whilst depth encompasses physiologically important factors such as light and temperature that drive community assembly (Diaz et al. 2023a); synchronous variations in biophysical factors across different reef sites also shape community structure (**Chapter 2, Chapter 3**) and ecological functions (**Chapter 4**), as well as the response of contemporary coral reef communities to recurring heat stress (**Chapter 3**).

The findings from this thesis have important implications for understanding both ecological and spatial resilience of coral reefs. How coral reef benthic communities reorganise following global scale disturbance events such as climate-induced warming events depends on the composition, distribution, and biological legacies (genetic composition, growth rates, thermal susceptibility, reproductive life history) of organisms and their interspecific interactions (Nyström and Folke 2001) that concurrently vary across depth gradients (**Chapter 2–3**). However, vertical zonation in the ecological memory of benthic communities adds another layer of complexity to understanding the interplay between disturbance and the adaptive dynamics of coral reefs assemblages; which is central to our understanding of how increasingly changing environmental conditions in the Anthropocene affect community organisation and ecosystem functioning (Karlson and Hurd 1993; Cresswell et al. 2023). For instance, the decreasing loss of hard and soft coral communities at greater depth (15–25 m) suggest potential depth refuge to thermal stress compared to communities at shallower gradients (5–15 m) (**Chapter 3**), but many functions that are provided by coral assemblages at depths, such as carbonate production rates intrinsically decrease with depth (**Chapter 4**).

Increasing biotic homogenisation of coral reefs at shallower depths raises important concerns about the ecosystem functions and resilience of tropical coral reefs (Aronson et al. 2005; Ford et al. 2023). Growing evidence from deeper reef zones (>20 m) (Smith et al. 2016; Sheppard et al. 2017; Muir et al. 2017; Morais and Santos 2018; Schramek et al. 2018; Frade et al. 2018; Baird et al. 2018; Crosbie et al. 2019; Venegas et al. 2019) indicate that whilst communities at depth occur in relatively more sheltered environments, they also show slower recovery than their shallow counterparts (**Chapter 4**, Sheppard et al. 2008, 2020). Characterised by lower recruitment rates (Turner et al. 2018; Roberts et al. 2019), the potential for reefs at depths to populate shallow reefs remains uncertain (Lesser et al. 2018).

As the duration, magnitude and severity of climate-driven thermal stress events scale-up, it is hypothesised that benthic communities at shallower depths (< 10 m) will show reduced recovery and may shift community distributions to deeper waters (Muir et al. 2017). However, it is also expected that increased ocean warming might disrupt important physical processes such as internal waves transporting cool, nutrient rich waters to shallow reef zones due to thermal stratification and deepening of the surface mixed layer (Freeland et al. 1997; Sallée et al. 2013). Whilst upwelling and internal wave activities may provide some protection against thermal stress and additional food subsidies that promote heterotrophy, especially when autotrophy is disrupted due to heat stress (Fox et al. 2023), other studies show that sustained thermal stratification and strong internal wave forcings can expose coral assemblages to temperatures below their temperature threshold (Wyatt 2019) and expose reefs to low oxygen and pH affecting coral communities and calcification rates at depths (Schmidt et al. 2012; Wall et al. 2012).

In addition to high spatial heterogeneity, coral reefs exhibit temporally complex dynamics. This thesis shows trends of benthic assemblages approaching a climax phase (Chapter 2), following the third global bleaching event (Chapter 3) and at the beginning of a potential recovery period (Chapter 4). It is evident that the benthic community of the Chagos Archipelago has transitioned through different successional stages since the 1998 massive bleaching event, i.e. recovered from minimal hard coral cover after severe bleaching (~12% in 1999; Sheppard, 1999) to a coral dominated community in 2013, where no significant divergence was apparent relative to pre-1998 communities (Sheppard et al. 2008, 2013b). For instance, scleractinian coral species, namely Acropora, Porites, Pocillopora that dominated both shallow and deep reef zones prior to the 1998 bleaching (Sheppard et al. 2008), correspond to the same generalist group observed in 2013 (Chapter 2) and in 2021/22 (Chapter 4). Despite recovery of dominant coral species following massive bleaching (Chapter 2-4) and no potential signs of regime shifted communities following multiple bleaching events (Chapter 3), significantly lower coral settlement (compared to larval settlement post-1998) on unfavourable substrate, such as dead crumbling coral skeletons and rubble (which increased with every bleaching event) and potential extinction of key coral species such as Isopora palifera highlight the uncertain effects of repeated bleaching on coral reefs (Sheppard et al. 2020).

5.3 Future directions research and recommendations

This thesis indicates heterogenous patterns and distribution of benthic community assemblages and geo-ecological functions across depth gradients on shallow coral reefs. Whilst depth was used as a proxy of biophysical factors that affect benthic community structure (**Chapter 2**), change in communities (**Chapter 3**) and ecosystem function (**Chapter 4**), including environmental data such as light, temperature, salinity from different depth zones would provide a more integrated understanding of the processes that drive the variation in benthic communities and the changes observed before and after bleaching among locations. Similarly, large scale oceanographic data across locations and depths such as wave exposure, upwelling and current regime could improve ecological models used to assess the change in benthic communities and ecosystem function spatially and temporally. Combining other ecological variables such as biological productivity, grazing fish biomass and other competitors would also provide a clearer evaluation of how the observed variability in benthic community composition influences wider ecological functioning.

A more accurate estimate of depth-dependent carbonate productivity could be provided by including calcification rates and skeletal density data from moderate depths. Additionally, by incorporating erosional processes (such as substrate grazing and endolithic boring) that vary across depths, a more complete assessment of vertical gradients in geo-ecological functions of coral reefs could be provided. In terms of method comparisons, inherent limitations in how *CoralNet* currently estimates coral carbonate production rates, e.g., availability of calcification rates for only few coral genera and morphotypes and calcification rates that automatically include erosional processes could be addressed by using customised coral production rates for all coral genera and morphotypes to reflect those from the *ReefBudget* method.

5.4 Conclusion

This thesis contributes to the understanding of the poorly described consistency in vertical zonation of benthic communities and ecosystem function in the context of systemic disturbances that are continuously altering tropical reef systems. The findings from this thesis show two clear patterns: 1) depth-dependent variation in benthic communities and hard coral assemblages and ecological function, 2) variation among atolls. By moving beyond the analysis of hard coral cover, the examination of the carbonate production side of reef budgets provided important insights into the zonation patterns of reef-building capacity of contemporary reefs,

and also indicated a potential recovery period is underway. However, as global climate change continues to alter coral reef ecosystems, it is becoming evidently difficult to explain and predict the environmental factors that naturally drive the reorganisation of benthic assemblages post-disturbance (Ford et al. 2023). For example, comparisons of benthic communities and coral assemblages following several disturbance events (including thermal stress events, cyclones and crown-of-thorn infestation) on reefs in the south Pacific (Moorea, Tahiti, Tetiaroa and Maiao) demonstrated variable effects of depth on community structure (Edmunds and Leichter 2016). Similarly, recent findings show trends of less predictable depth zonation patterns in reef fish communities on reefs impacted by pervasive stressors (Richardson et al. 2023) and increasingly non-linear rates of recovery in the face of recurring widespread disturbance events (Cresswell et al. 2023). Building on evidence from the wider Indo-Pacific and this thesis, incorporating deeper communities across different locations in coral reef surveys will be essential to our understanding of ecological and functional dynamics of increasingly disturbed shallow coral reefs.

Automatic citation updates are disabled. To see the bibliography, click Refresh in the Zotero tab.

Appendix A - Supplementary materials for Chapter 2: Atoll-dependent depth variation in depth zonation of benthic communities on remote reefs

Atoll		Island	Position	Lat (deg min)	Long (deg min)
Great Bank	Chagos	Nelson Island	South	5:40:769	72:18:906
Great Bank	Chagos	Eagle Island South	South	6:11:950	71:18:942
Great Bank	Chagos	Middle Brother	South	6 09.429	71 30.652
Egmont	t	North	South	6:38:096	71:19:645
Egmont	t	Middle	South	6 38.604	71 21.488
Egmont South		South	6:40.812	71:23.730	
Peros Banhos Ile Petite Coquillage		North	5:20:510	71:58:800	
Peros B	anhos	Ile Fouquet	North	5 27.900	71 49.100
Salomo	n	Ile Anglaise South	North	5 20.300	72 12.740
Salomon		Ile Anglaise South Tip	North	5:20:370	72:12:750
Salomo	n	Ile Anglaise South Pass	North	5 20.300	72 12.740
Salomo	n	Ile Anglaise Middle	North	5:19:900	72:13:150
Salomon Takamaka		North	5:20:050	72:16:890	

Table S1: List of sites (with coordinates) surveyed in the Chagos Archipelago in 2013.

Table S2: Multivariate dispersion among- and within-atoll in major functional groups between shallow reef slopes (5–10 m) and deep reef slopes (20–25 m) at Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

	PseudoF-ratio	df	p-value
Among-atoll	6.99	7,772	0.001
Within-atoll			
EG	8.475	1, 178	0.006
GCB	1.002	1, 178	0.303
PB	21.075	1, 118	0.001
SA	2.124	1, 298	0.145

Table S3: Multivariate dispersion among- atolls in hard coral assemblage between shallow reef slopes (5–10 m) and deep reef slopes (20–25 m) at Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

	PseudoF-ratio	df	p-value
Among-atoll	16.4	7,643	0.001
Within-atoll			
EG	3.81	1, 155	0.056
GCB	1.309	1, 159	0.256
PB	68.415	1,94	0.001
SA	31.483	1, 275	0.001
Table S4: Mean \pm SE proportional cover (%) of major functional groups across depths (5–10 m and 20–25 m) and atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) in the Chagos Archipelago in 2013.

Atoll	EG						GCB						PB						SA					
Depth	5–10 n	n		25–25	m		5–10 n	1		25–25	m		5–10 n	n		25–25 1	m		5–	10 m		25-	-25 1	n
Bare substrate	19.26	±	2.13	1.63	±	0.49	20.37	±	1.60	14.89	±	1.88	10.78	±	1.42	9.89	±	2.01	14.71	±	1.24	8.89	±	0.91
Bleached coral	0.15	±	0.10	0.00	±	0.00	0.44	±	0.21	0.15	±	0.10	0.00	±	0.00	0.11	±	0.11	0.27	±	0.19	0.00	±	0.00
CCA	8.81	±	1.07	29.04	±	1.87	13.70	±	1.72	14.30	±	1.40	18.44	±	2.02	14.89	±	1.92	10.62	±	0.89	16.53	±	1.18
Dead coral	8.07	±	1.31	1.56	±	0.45	10.89	±	1.69	6.67	±	1.42	10.44	±	1.86	0.67	±	0.30	14.98	±	1.42	3.20	±	0.46
Disease	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Hard coral	18.89	±	1.99	8.07	±	1.36	26.89	±	2.50	32.07	±	2.49	43.33	±	2.42	8.11	±	1.22	33.51	±	1.87	25.47	±	1.69
Macroalgae	0.30	±	0.15	2.59	±	0.53	0.52	±	0.32	0.81	±	0.42	0.78	±	0.32	4.33	±	1.23	0.22	±	0.10	1.82	±	0.31
Non- scleractinian	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04	0.13	±	0.13
Other live	0.30	±	0.15	1.26	±	0.35	0.37	±	0.16	1.11	±	0.40	0.11	±	0.11	1.11	±	0.51	0.13	±	0.08	2.49	±	0.64
Sand&rubble	2.52	±	0.48	6.89	±	1.06	5.11	±	1.02	9.26	±	1.23	1.78	±	0.52	14.89	±	2.51	1.24	±	0.42	2.93	±	0.57
Soft coral	1.19	±	0.45	1.63	±	0.50	0.74	±	0.32	2.67	±	0.67	4.00	±	0.95	9.78	±	1.65	4.93	±	0.61	12.67	±	1.37
Sponges	3.48	±	0.72	11.85	±	1.12	4.52	±	0.84	4.00	±	0.77	2.44	±	0.63	13.11	±	1.91	7.60	±	0.98	11.11	±	1.11

Turf	35.33	±	2.68	33.85	±	2.04	14.52	±	1.84	11.48	±	1.87	6.00	±	1.25	21.33	±	2.12	7.73	±	1.02	11.47	±	1.18
Unknown	1.70	±	0.40	1.63	±	0.38	1.93	±	0.47	2.59	±	0.59	1.89	±	0.57	1.78	±	0.47	4.00	±	0.58	3.29	±	0.53

Table S5: Mean proportional cover \pm se (%) of coral genera observed across atolls - Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA), at shallow reef slopes (5–10 m) and deep reef slopes (20–25 m) in 2013. In *bold* are the indicator coral genera that characterised each depth at each atoll.

Atoll	EG				GCB						PB						SA					
Depth	5–10 m	25-	-25 m		5–10 r	m		25-25	5 m		5-10	m		25-25	m		5-10	m		25-25	5 m	
Acanthastrea	0.00 ± 0.00	0.00 0.0	± 0	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.09	±	0.04
Acropora	0.45 ± 0	0.82 0.1	7 ±	0.09	4.35	±	0.82	4.00	±	0.66	2.56	±	0.54	0.04	±	0.04	5.39	±	0.65	1.60	±	0.31
Alveopora- Goniopora	0.00 ± 0	0.02 0.0	± 0	0.00	0.02	±	0.02	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Astreopora	0.00 ± 0.00	0.00 0.0	± 0	0.00	0.00	±	0.00	0.00	±	0.00	0.06	±	0.06	0.06	±	0.06	0.07	±	0.05	0.02	±	0.02
Caryophyllia	0.00 ± 0.00	0.00 0.0	7 ±	0.07	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04
Caulastrea	0.00 ± 0.00	0.00 0.0	± 0	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04	0.00	±	0.00
Cyphastrea	0.00 ± 0.00	0.00 0.0	4 ±	0.04	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Diploastrea	0.00 ± 0.00	0.00 0.0	± 0	0.00	0.00	±	0.00	0.00	±	0.00	0.11	±	0.11	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Echinopora	0.00 ± 0	0.00 0.0	± 0	0.00	0.00	±	0.00	0.41	±	0.20	0.00	±	0.00	0.11	\pm	0.11	0.00	±	0.00	0.00	±	0.00

Favia	0.11	±	0.07	0.00	±	0.00	0.12	±	0.07	0.10	±	0.07	0.11	±	0.08	0.00	±	0.00	0.06	±	0.03	0.07	±	0.04
Favites	0.05	±	0.09	0.15	±	0.09	0.15	±	0.09	0.07	±	0.05	0.06	±	0.06	0.00	±	0.00	0.04	±	0.03	0.11	±	0.07
Galaxea	0.00	±	0.02	0.00	±	0.00	0.02	±	0.02	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.01	±	0.01
Gardineroseris	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.26	±	0.23	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04	0.04	±	0.03
Goniastrea	0.02	±	0.00	0.00	±	0.00	0.00	±	0.00	0.07	±	0.04	0.19	±	0.19	0.00	±	0.00	0.01	±	0.01	0.21	±	0.07
Herpolitha	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.07	±	0.07	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Leptastrea	0.08	±	0.00	0.00	±	0.00	0.00	±	0.00	0.22	±	0.14	0.00	±	0.00	0.06	±	0.06	0.00	±	0.00	0.00	±	0.00
Leptoria	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.02	±	0.02
Leptoseris	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04	0.00	±	0.00	0.00	±	0.00	0.04	±	0.03	0.09	±	0.05
Lobophyllia	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04	0.00	±	0.00
Montipora	0.04	±	0.07	0.00	±	0.00	0.11	±	0.07	0.22	±	0.09	0.06	±	0.04	0.06	±	0.04	0.12	±	0.05	0.64	±	0.17
Oulophyllia	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04
Pachyseris	0.00	±	0.02	0.49	±	0.33	0.02	±	0.02	0.59	±	0.24	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	1.07	±	0.29
Pavona	0.00	±	0.06	0.22	±	0.09	0.07	±	0.06	0.13	±	0.06	0.00	±	0.00	0.08	±	0.08	0.04	±	0.02	0.10	±	0.04
Phymastrea	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.04	±	0.04	0.00	±	0.00	0.11	±	0.11	0.00	±	0.00	0.04	±	0.04
Platygyra	0.04	±	0.04	0.07	±	0.07	0.04	±	0.04	0.15	±	0.12	0.00	±	0.00	0.00	±	0.00	0.09	±	0.05	0.02	±	0.02
Plerogyra	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.13	±	0.13

Plesiastrea	0.00	±	0.00	0.04	±	0.04	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Pocillopora	0.27	±	0.22	0.26	±	0.15	0.74	±	0.22	0.93	±	0.41	1.06	±	0.34	0.33	±	0.23	0.71	±	0.15	0.27	±	0.08
Podabacia	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.07	±	0.07	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.09	±	0.09
Polyphyllia	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.11	±	0.11	0.00	±	0.00	0.04	±	0.04
Porites	0.21	<u>+</u>	0.21	0.16	±	0.06	1.02	±	0.21	0.84	±	0.23	4.26	±	0.61	0.37	±	0.15	1.31	<u>+</u>	0.19	1.01	±	0.20
Poritipora	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.22	±	0.22	0.11	±	0.11	0.00	±	0.00	0.00	±	0.00
Seriatopora	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.33	±	0.27	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.38	±	0.12
Stylophora	0.04	<u>+</u>	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.56	±	0.19	0.00	±	0.00	0.31	<u>+</u>	0.10	0.02	±	0.02
Symphyllia	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.63	±	0.31	0.00	±	0.00	0.06	±	0.06	0.00	±	0.00	0.04	±	0.04
Tubastraea	0.00	<u>+</u>	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	1.11	±	0.33	0.00	<u>+</u>	0.00	0.00	±	0.00
Turbinaria	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.11	±	0.11	0.00	±	0.00	0.00	±	0.00	0.03	±	0.02
Other	0.07	±	0.09	0.30	±	0.06	0.45	±	0.09	0.41	±	0.08	0.48	±	0.09	0.11	±	0.04	0.59	±	0.07	0.46	±	0.06

Other - un-identified coral genera



Figure S1: Non-metric dimensional scaling (nMDS) of major functional groups showing clustering by atolls, based on Bray-Curtis dissimilarities of square-root transformed data in a total of 26 sites in the Chagos Archipelago. Coloured ellipses represent dispersion of atolls centroids 95% confidence at limit Egmont (EG), Great Chagos Bank _ (GCB), Peros Banhos (PB) and Salomon (SA). Coloured symbols represent different atolls at depth - grey: 5-10 m and black:25-25 m. Vectors represent major functional groups distribution to the patterns on the ordination plot (red labels indicate a significant contribution and black labels indicate a non-significant contribution).



Figure S2: Non-metric dimensional scaling (nMDS) of coral genera assemblage showing clustering by atolls, based on Bray-Curtis dissimilarities of square-root transformed data in a total of 26 sites in the Chagos Archipelago. Coloured ellipses represent dispersion of atolls centroids at 95% confidence limit – Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Coloured symbols represent different atolls at depth – grey: 5–10 m and black:25–25 m. Vectors represent 1) major functional groups (left) and 2) coral genera (right) distribution to the patterns on the ordination plot.

Appendix B - Supplementary materials for Chapter 3: Depth variation in benthic community response to repeated thermal stress on remote reefs

Atoll	Site	Latitude	Longitude	DHW	
71011	Site	Lutitude	Longitude	Initial	Cumulative
Famont	Middle	-6.636	71.318	4.48	20.7
Eginoin	North	-6.635	71.363	3.99	20.13
~	Dangle Is	-6.386	71.235	4.11	19.04
Great	Middle Brother	-6.136	71.521	5.27	21.09
Bank	Nelson Is Middle	-5.669	72.303	5.9	19.87
	South Brother	-6.177	71.540	5.25	21.02
	Ile Diamant	-5.235	71.771	4.94	17.63
	Ile Fouquet	-5.240	71.802	5.2	18.13
Dama	Moresby	-5.453	71.819	5.14	17.84
Peros Banhos	Ile Passe	-5.348	71.969	5.14	17.84
Dumos	Ile Poule	-5.398	71.749	4.67	17.08
	Petite Ile Coquillage	-5.240	71.836	5.32	17.64
	Ile Yeye	-5.252	71.975	5.51	18.29
	Ile Anglaise South Tip	-5.286	72.259	5.85	18.27
Salomon	Ile Passe	-5.344	72.202	6.36	18.98
	Takamaka	-5.347	72.269	6.17	18.74

Table S1: List of surveyed sites and initial and cumulative DHW across sampled sites

Table S2: List of linear regression models and prior specifications

Change in benthic group cover_i ~ Normal (μ_i, σ_i)

 $\mu_{i} = \beta_{j[i]} + \beta_{1}(\text{depth x atoll x DHW2015}) + \beta_{2}(\text{depth x atoll x cumDHW}) + \gamma_{s[i]}$

Benthic groups	Prior specification
Hard coral Δ Hard coral cover _i ~ Normal (μ_i , σ_i)	$\beta_{j[i]} \sim N (0, 0.2)$ [depth-specific intercepts: for each depth zone j in (1j)] $\beta_N \sim N (0, 0.2)$ $\gamma_{s[i]} \sim N (0, 2.5)$ [Offsets for grouping variable: site, s, nested in atoll] $\sigma_i \sim N (0, 2.5)$
Soft coral Δ Soft coral cover _i ~ Normal (μ _i , σ _i)	$ \begin{array}{l} \beta_{j[i]} \sim N \ (0, \ 0.2) \\ \beta_{N} \sim N \ (0, \ 0.2) \\ \gamma_{i} \sim N \ (0, \ 2.5) \\ \sigma_{i} \sim N \ (0, \ 2.5) \end{array} $

CCA Δ CCA cover _i ~ Normal (μ_i , σ_i)	$ \begin{array}{l} \beta_{j[i]} \sim N \ (0, \ 0.2) \\ \beta_{N} \sim N \ (0, \ 0.2) \\ \gamma_{i} \sim N \ (0, \ 2.5) \\ \sigma_{i} \sim N \ (0, \ 2.5) \end{array} $
Sponge Δ Sponge cover _i ~ Normal (μ _i , σ _i)	$ \begin{array}{l} \beta_{j[i]} \sim N \; (0, \; 0.3) \\ \beta_{N} \sim N \; (0, \; 0.3) \\ \gamma_{i} \sim N \; (0, \; 2.5) \\ \sigma_{i} \sim N \; (0, \; 2.5) \end{array} $
Reef pavement Δ Reef pavement cover _i ~ Normal (μ_i , σ_i)	$ \begin{array}{l} \beta_{j[i]} \sim N \ (0, \ 0.2) \\ \beta_{N} \sim N \ (0, \ 0.2) \\ \gamma_{i} \sim N \ (0, \ 2.5) \\ \sigma_{i} \sim N \ (0, \ 2.5) \end{array} $

Note: The brms package automatically truncates the prior specification for σ , γ and allow only positive values

Table	S3:	Bonferroni	pairwise	comparisons	of benthic	community	composition	before	(pre)
versus	afte	er (post) 201	5–2017 n	narine heatwa	ives across	depth and an	nong atolls.		

		Pairwise comparis	sons		F ratio	R2	pval	p.adj
		5-10m_post	vs	5-10m_pre	32.04888	0.51651	0.001	0.028
Heatwaves	х	10-15m_post	VS	10-15m_pre	25.80656	0.462429	0.001	0.028
Depth		15-20m_post	VS	15-20m_pre	15.70015	0.343547	0.001	0.028
		20-25m_post	VS	20-25m_pre	4.005531	0.117791	0.008	0.224
		EG_post	VS	EG_pre	1.355512	0.088275	0.277	1
Heatwaves	х	GCB_post	VS	GCB_pre	21.13309	0.413296	0.001	0.028
Atoll		PB_post	VS	PB_pre	20.00465	0.270316	0.001	0.028
		SA_post	VS	SA_pre	20.24629	0.479244	0.001	0.028

Table S4: Posterior predicted change in benthic groups (mean \pm SE) following the 2015–2017 marine heatwaves and standardised effects of change in benthic groups across four depth zones at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). In bold are weak (50% CI) and strong (95% CI) effects of depth on change in benthic group cover among atolls. Depth effects can be visualised in Supplementary material, Figure S3.

			Change	in co	over	Effort	50%		95%	
	Depth	Atoll	Moon +	SE ((0/2)	sizes	Lower	Upper	Lower	Upper
				SE ((%)	51265	CI	CI	CI	CI
		EG	6.93	\pm	1.27	-0.21	-0.29	-0.14	-0.41	0.01
	5 10m	GCB	-38.14	\pm	4.42	-0.62	-0.68	-0.58	-0.77	-0.46
	J-10111	PB	-15.83	\pm	1.66	-0.05	-0.10	0.02	-0.23	0.13
		SA	-10.89	±	1.98	-0.07	-0.16	0.03	-0.35	0.20
		EG	0.69	\pm	1.65	-0.23	-0.31	-0.12	-0.49	0.06
	10.15m	GCB	-28.80	\pm	5.57	-0.54	-0.61	-0.49	-0.72	-0.36
ral	10-1311	PB	-13.63	\pm	1.91	0.00	-0.07	0.10	-0.25	0.24
CO		SA	-16.30	\pm	0.94	-0.16	-0.29	-0.03	-0.54	0.22
ard		EG	-0.49	\pm	1.52	-0.22	-0.31	-0.12	-0.51	0.05
H	15.20m	GCB	-18.65	\pm	7.43	-0.47	-0.55	-0.42	-0.66	-0.27
	13-2011	PB	-12.84	\pm	1.74	-0.02	-0.11	0.06	-0.26	0.24
		SA	-14.17	±	0.88	-0.13	-0.25	0.00	-0.51	0.25
		EG	7.96	\pm	2.49	-0.19	-0.28	-0.09	-0.48	0.08
	20.25m	GCB	-17.31	\pm	7.26	-0.41	-0.46	-0.35	-0.59	-0.22
	20-23111	PB	-9.58	\pm	1.98	0.08	-0.01	0.16	-0.18	0.32
		SA	-10.37	\pm	2.69	-0.09	-0.23	0.04	-0.47	0.29
		EG	-12.91	\pm	12.65	-0.14	-0.29	0.00	-0.55	0.29
	5 10m	GCB	-83.98	\pm	3.83	-0.99	-1.14	-0.86	-1.39	-0.58
	J-10111	PB	-29.91	\pm	10.61	-0.51	-0.61	-0.38	-0.85	-0.17
		SA	-22.96	\pm	29.68	-0.47	-0.59	-0.34	-0.83	-0.11
		EG	-2.29	\pm	7.36	-0.03	-0.21	0.16	-0.60	0.50
	10.15m	GCB	-38.71	\pm	7.09	0.07	-0.10	0.28	-0.47	0.63
al	10-1311	PB	-33.27	\pm	5.44	-0.32	-0.50	-0.18	-0.79	0.15
COI		SA	-17.14	±	5.64	-0.22	-0.39	-0.04	-0.74	0.28
oft		EG	-16.25	\pm	2.63	-0.20	-0.32	-0.07	-0.55	0.19
Š	15.20m	GCB	-4.77	\pm	13.71	-0.06	-0.16	0.09	-0.43	0.31
	13-2011	PB	-19.82	\pm	2.70	-0.32	-0.43	-0.21	-0.65	0.02
		SA	-32.38	\pm	4.19	-0.33	-0.48	-0.20	-0.71	0.12
		EG	-8.94	\pm	11.04	-0.05	-0.18	0.06	-0.42	0.33
	20.25m	GCB	-20.66	\pm	9.09	0.04	-0.06	0.19	-0.37	0.41
	20-23111	PB	-3.22	\pm	4.17	-0.16	-0.29	-0.06	-0.52	0.16
		SA	-21.05	\pm	3.16	-0.14	-0.27	0.01	-0.57	0.25
		EG	4.44	\pm	2.91	0.09	0.00	0.17	-0.16	0.35
	5 10m	GCB	13.65	\pm	7.01	0.14	0.05	0.22	-0.14	0.39
	J-10111	PB	7.12	\pm	4.03	-0.05	-0.14	0.04	-0.30	0.21
ÇA		SA	11.97	±	2.99	0.08	-0.03	0.18	-0.21	0.38
ŭ		EG	8.67	±	2.29	0.07	-0.03	0.20	-0.29	0.41
	10_15m	GCB	6.13	\pm	4.00	0.02	-0.09	0.14	-0.33	0.37
	10-1311	PB	13.74	\pm	7.13	-0.10	-0.23	0.01	-0.45	0.26
		SA	18.98	±	4.06	0.14	-0.02	0.27	-0.25	0.58

		EG	3.83	\pm	2.14	0.06	-0.06	0.15	-0.26	0.35
	15 20	GCB	-4.12	\pm	4.48	0.04	-0.04	0.15	-0.25	0.34
	15-20m	PB	9.32	\pm	3.05	-0.01	-0.13	0.10	-0.35	0.32
		SA	13.07	\pm	1.78	0.07	-0.06	0.22	-0.33	0.48
		EG	1.74	\pm	2.39	-0.06	-0.19	0.06	-0.45	0.30
	20.25	GCB	3.33	\pm	9.56	-0.13	-0.25	0.01	-0.55	0.24
	20-25m	PB	-8.35	\pm	6.84	-0.26	-0.38	-0.12	-0.61	0.14
		SA	7.69	\pm	6.27	0.01	-0.11	0.19	-0.43	0.44
		EG	11.60	±	5.26	0.09	0.01	0.15	-0.12	0.30
	5 10	GCB	19.40	\pm	3.49	0.12	0.06	0.17	-0.04	0.28
	5-10m	PB	10.12	\pm	2.25	0.03	-0.04	0.09	-0.17	0.23
		SA	12.12	<u>±</u>	3.73	0.10	-0.01	0.18	-0.19	0.39
		EG	18.31	±	12.13	0.16	0.06	0.27	-0.15	0.49
nt	10.15m	GCB	12.65	\pm	2.27	0.13	0.06	0.22	-0.12	0.39
neı	10-13111	PB	12.39	\pm	4.49	0.11	0.01	0.21	-0.21	0.40
vei		SA	17.36	<u>±</u>	6.54	0.19	0.06	0.34	-0.25	0.59
, pa		EG	33.55	±	14.26	0.16	0.09	0.29	-0.13	0.45
eef	15.20m	GCB	14.34	\pm	4.11	0.04	-0.02	0.10	-0.17	0.23
R	13-2011	PB	7.47	\pm	2.45	0.06	-0.05	0.13	-0.18	0.34
		SA	13.12	\pm	6.12	0.24	0.11	0.37	-0.16	0.63
		EG	65.27	\pm	3.67	0.18	0.08	0.28	-0.12	0.46
	20.25m	GCB	4.78	\pm	2.45	-0.02	-0.08	0.05	-0.22	0.19
	20-23111	PB	8.50	\pm	3.82	0.02	-0.11	0.09	-0.24	0.34
		SA	-0.80	\pm	2.19	0.12	-0.01	0.26	-0.27	0.52
					=,	0.12	0.01	0.20	0.11 /	0.01
		EG	10.87	±	2.85	0.12	0.11	0.34	-0.11	0.57
	5 10m	EG GCB	10.87 52.57	± ±	2.85 11.65	0.12 0.22 0.48	0.11 0.40	0.34 0.57	-0.11 0.20	0.57 0.73
	5-10m	EG GCB PB	10.87 52.57 25.22	± ± ±	2.85 11.65 5.20	0.12 0.22 0.48 0.13	0.01 0.11 0.40 0.01	0.34 0.57 0.23	-0.11 0.20 -0.18	0.57 0.73 0.45
	5-10m	EG GCB PB SA	10.87 52.57 25.22 33.32	± ± ±	2.85 11.65 5.20 6.87	0.12 0.22 0.48 0.13 0.21	0.01 0.11 0.40 0.01 0.06	0.34 0.57 0.23 0.35	-0.11 0.20 -0.18 -0.20	0.57 0.73 0.45 0.64
	5-10m	EG GCB PB SA EG	10.87 52.57 25.22 33.32 9.93	± ± ± ±	2.85 11.65 5.20 6.87 1.07	0.12 0.22 0.48 0.13 0.21 0.17	0.01 0.11 0.40 0.01 0.06 0.00	0.34 0.57 0.23 0.35 0.31	-0.11 0.20 -0.18 -0.20 -0.29	0.57 0.73 0.45 0.64 0.64
	5-10m	EG GCB PB SA EG GCB	10.87 52.57 25.22 33.32 9.93 52.63	+ + + + + +	2.85 11.65 5.20 6.87 1.07 23.85	0.12 0.22 0.48 0.13 0.21 0.17 0.50	0.01 0.11 0.40 0.01 0.06 0.00 0.37	0.34 0.57 0.23 0.35 0.31 0.60	-0.11 0.20 -0.18 -0.20 -0.29 0.13	0.57 0.73 0.45 0.64 0.64 0.85
G	5-10m 10-15m	EG GCB PB SA EG GCB PB	10.87 52.57 25.22 33.32 9.93 52.63 23.32	+ + + + + + +	2.85 11.65 5.20 6.87 1.07 23.85 9.03	0.12 0.22 0.48 0.13 0.21 0.17 0.50 -0.03	0.01 0.11 0.40 0.01 0.06 0.00 0.37 -0.20	0.34 0.57 0.23 0.35 0.31 0.60 0.09	-0.11 0.20 -0.18 -0.20 -0.29 0.13 -0.46	0.57 0.73 0.45 0.64 0.64 0.85 0.42
nge	5-10m 10-15m	EG GCB PB SA EG GCB PB SA	10.87 52.57 25.22 33.32 9.93 52.63 23.32 16.08	+ + + + + +	2.85 11.65 5.20 6.87 1.07 23.85 9.03 8.10	0.12 0.22 0.48 0.13 0.21 0.17 0.50 -0.03 0.16	$\begin{array}{r} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38	-0.11 0.20 -0.18 -0.20 -0.29 0.13 -0.46 -0.46	0.57 0.73 0.45 0.64 0.64 0.85 0.42 0.74
Sponge	5-10m 10-15m	EG GCB PB SA EG GCB PB SA EG	10.87 52.57 25.22 33.32 9.93 52.63 23.32 16.08 0.64	+ + + + + + + + +	2.85 11.65 5.20 6.87 1.07 23.85 9.03 8.10 4.89	0.12 0.22 0.48 0.13 0.21 0.17 0.50 -0.03 0.16 0.10	$\begin{array}{r} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38 0.26	-0.11 0.20 -0.18 -0.20 -0.29 0.13 -0.46 -0.46 -0.31	0.57 0.73 0.45 0.64 0.64 0.64 0.85 0.42 0.74 0.54
Sponge	5-10m 10-15m	EG GCB PB SA EG GCB PB SA EG GCB	10.87 52.57 25.22 33.32 9.93 52.63 23.32 16.08 0.64 10.00	+ + + + + + + + +	2.85 11.65 5.20 6.87 1.07 23.85 9.03 8.10 4.89 6.66	$\begin{array}{c} 0.12\\ 0.22\\ 0.48\\ 0.13\\ 0.21\\ 0.17\\ 0.50\\ -0.03\\ 0.16\\ 0.10\\ 0.20\\ \end{array}$	$\begin{array}{c} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ 0.09\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38 0.26 0.31	$\begin{array}{r} -0.11\\ 0.20\\ -0.18\\ -0.20\\ -0.29\\ 0.13\\ -0.46\\ -0.46\\ -0.31\\ -0.11\\ \end{array}$	0.57 0.73 0.45 0.64 0.64 0.85 0.42 0.74 0.54 0.51
Sponge	5-10m 10-15m 15-20m	EG GCB PB SA EG GCB PB SA EG GCB PB	10.87 52.57 25.22 33.32 9.93 52.63 23.32 16.08 0.64 10.00 10.82	+ + + + + + + + + + +	2.85 11.65 5.20 6.87 1.07 23.85 9.03 8.10 4.89 6.66 4.40	$\begin{array}{c} 0.12\\ 0.22\\ 0.48\\ 0.13\\ 0.21\\ 0.17\\ 0.50\\ -0.03\\ 0.16\\ 0.10\\ 0.20\\ -0.10\\ \end{array}$	$\begin{array}{r} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ 0.09\\ -0.25\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38 0.26 0.31 0.04	$\begin{array}{r} -0.11\\ 0.20\\ -0.18\\ -0.20\\ -0.29\\ 0.13\\ -0.46\\ -0.46\\ -0.31\\ -0.11\\ -0.51\\ \end{array}$	0.57 0.73 0.45 0.64 0.64 0.85 0.42 0.74 0.54 0.51 0.33
Sponge	5-10m 10-15m 15-20m	EG GCB PB SA EG GCB PB SA EG GCB PB SA	$\begin{array}{c} 10.87\\ 52.57\\ 25.22\\ 33.32\\ 9.93\\ 52.63\\ 23.32\\ 16.08\\ 0.64\\ 10.00\\ 10.82\\ 21.40\\ \end{array}$	+ + + + + + + + + + +	$\begin{array}{c} 2.85\\ 11.65\\ 5.20\\ 6.87\\ 1.07\\ 23.85\\ 9.03\\ 8.10\\ 4.89\\ 6.66\\ 4.40\\ 6.37\\ \end{array}$	$\begin{array}{c} 0.12 \\ 0.22 \\ 0.48 \\ 0.13 \\ 0.21 \\ 0.17 \\ 0.50 \\ -0.03 \\ 0.16 \\ 0.10 \\ 0.20 \\ -0.10 \\ 0.09 \end{array}$	$\begin{array}{c} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ 0.09\\ -0.25\\ -0.15\\ \end{array}$	$\begin{array}{c} 0.34\\ 0.57\\ 0.23\\ 0.35\\ \hline 0.31\\ 0.60\\ 0.09\\ \hline 0.38\\ 0.26\\ 0.31\\ 0.04\\ 0.27\\ \end{array}$	$\begin{array}{r} -0.11\\ 0.20\\ -0.18\\ -0.20\\ -0.29\\ 0.13\\ -0.46\\ -0.46\\ -0.31\\ -0.11\\ -0.51\\ -0.52\\ \end{array}$	$\begin{array}{c} 0.52 \\ \hline 0.57 \\ 0.73 \\ 0.45 \\ \hline 0.64 \\ \hline 0.64 \\ 0.85 \\ 0.42 \\ \hline 0.74 \\ \hline 0.54 \\ 0.51 \\ 0.33 \\ \hline 0.65 \end{array}$
Sponge	5-10m 10-15m 15-20m	EG GCB PB SA EG GCB PB SA EG SA EG	10.87 52.57 25.22 33.32 9.93 52.63 23.32 16.08 0.64 10.00 10.82 21.40 -0.54	+ + + + + + + + + + + + + + + + + + + +	$\begin{array}{c} 2.85\\ 2.85\\ 11.65\\ 5.20\\ 6.87\\ 1.07\\ 23.85\\ 9.03\\ 8.10\\ 4.89\\ 6.66\\ 4.40\\ 6.37\\ 3.23 \end{array}$	$\begin{array}{c} 0.12 \\ 0.22 \\ 0.48 \\ 0.13 \\ 0.21 \\ 0.17 \\ 0.50 \\ -0.03 \\ 0.16 \\ 0.10 \\ 0.20 \\ -0.10 \\ 0.09 \\ 0.05 \end{array}$	$\begin{array}{r} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ 0.09\\ -0.25\\ -0.15\\ -0.11\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38 0.26 0.31 0.04 0.27 0.18	-0.11 0.20 -0.18 -0.20 -0.29 0.13 -0.46 -0.46 -0.46 -0.31 -0.11 -0.51 -0.52 -0.39	$\begin{array}{c} 0.52 \\ \hline 0.57 \\ 0.73 \\ 0.45 \\ \hline 0.64 \\ 0.64 \\ \hline 0.85 \\ 0.42 \\ \hline 0.74 \\ \hline 0.54 \\ 0.51 \\ \hline 0.33 \\ \hline 0.65 \\ \hline 0.45 \end{array}$
Sponge	5-10m 10-15m 15-20m	EG GCB PB SA EG GCB PB SA EG GCB PB SA EG GCB	$\begin{array}{c} 10.87\\ 52.57\\ 25.22\\ 33.32\\ 9.93\\ 52.63\\ 23.32\\ 16.08\\ 0.64\\ 10.00\\ 10.82\\ 21.40\\ -0.54\\ 4.57\\ \end{array}$	+ + + + + + + + + + + + + + + + + + +	$\begin{array}{c} 2.85\\ 11.65\\ 5.20\\ 6.87\\ 1.07\\ 23.85\\ 9.03\\ 8.10\\ 4.89\\ 6.66\\ 4.40\\ 6.37\\ 3.23\\ 4.09\end{array}$	$\begin{array}{c} 0.12\\ 0.22\\ 0.48\\ 0.13\\ 0.21\\ 0.17\\ 0.50\\ -0.03\\ 0.16\\ 0.10\\ 0.20\\ -0.10\\ 0.20\\ -0.10\\ 0.09\\ 0.05\\ 0.08\\ \end{array}$	$\begin{array}{c} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ 0.09\\ -0.25\\ -0.15\\ -0.11\\ -0.01\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38 0.26 0.31 0.04 0.27 0.18	$\begin{array}{r} -0.11\\ 0.20\\ -0.18\\ -0.20\\ -0.29\\ 0.13\\ -0.46\\ -0.46\\ -0.31\\ -0.11\\ -0.51\\ -0.52\\ -0.39\\ -0.21\\ \end{array}$	$\begin{array}{c} 0.52 \\ \hline 0.57 \\ 0.73 \\ 0.45 \\ \hline 0.64 \\ 0.85 \\ 0.42 \\ \hline 0.74 \\ 0.54 \\ 0.51 \\ 0.33 \\ \hline 0.65 \\ 0.45 \\ 0.39 \end{array}$
Sponge	5-10m 10-15m 15-20m 20-25m	EG GCB PB SA EG GCB PB SA EG GCB PB SA EG GCB PB	$\begin{array}{c} 10.87\\ 52.57\\ 25.22\\ 33.32\\ 9.93\\ 52.63\\ 23.32\\ 16.08\\ 0.64\\ 10.00\\ 10.82\\ 21.40\\ -0.54\\ 4.57\\ 5.63\\ \end{array}$	+ + + + + + + + + + + + + + + + + + + +	$\begin{array}{c} 2.85\\ 2.85\\ 11.65\\ 5.20\\ 6.87\\ 1.07\\ 23.85\\ 9.03\\ 8.10\\ 4.89\\ 6.66\\ 4.40\\ 6.37\\ 3.23\\ 4.09\\ 4.24 \end{array}$	$\begin{array}{c} 0.12\\ 0.22\\ 0.48\\ 0.13\\ 0.21\\ 0.17\\ 0.50\\ -0.03\\ 0.16\\ 0.10\\ 0.20\\ -0.10\\ 0.20\\ -0.10\\ 0.09\\ 0.05\\ 0.08\\ 0.00\\ \end{array}$	$\begin{array}{c} 0.01\\ 0.11\\ 0.40\\ 0.01\\ 0.06\\ 0.00\\ 0.37\\ -0.20\\ -0.05\\ -0.04\\ 0.09\\ -0.25\\ -0.15\\ -0.11\\ -0.01\\ -0.13\\ \end{array}$	0.34 0.57 0.23 0.35 0.31 0.60 0.09 0.38 0.26 0.31 0.04 0.27 0.18 0.14	$\begin{array}{r} -0.11\\ 0.20\\ -0.18\\ -0.20\\ -0.29\\ 0.13\\ -0.46\\ -0.46\\ -0.46\\ -0.31\\ -0.51\\ -0.51\\ -0.52\\ -0.39\\ -0.21\\ -0.41\\ \end{array}$	0.57 0.73 0.45 0.64 0.64 0.85 0.42 0.74 0.54 0.51 0.33 0.65 0.45 0.39 0.39

Table S5: Standardised effects of a) initial and b) repeated thermal stress on change in cover of benthic groups following the 2015–2017 marine heatwaves across depth zones at four atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). In bold are weak (50% CI) and strong effects (95% CI) of thermal stress on change in benthic groups among atolls.

	a) Depth Atoll Change in cover Initial 50% Mean + SE (%) effects Low	50%	95%							
a)	Depth	Atoll	Mean ±	SE	(%)	effects	Lower	Upper	Lower	Upper
		FC	6.02		1.07	0.12	0.10			
		EG	6.93	±	1.27	-0.13	-0.18	-0.08	-0.29	0.03
	5-10m	GCB	-38.14	±	4.42	-0.22	-0.27	-0.19	-0.34	-0.08
		PB	-15.83	±	1.66	-0.22	-0.29	-0.12	-0.47	0.04
_		SA	-10.89	±	1.98	-0.06	-0.15	0.04	-0.31	0.22
		EG	0.69	±	1.65	-0.06	-0.14	0.01	-0.27	0.15
	10-	GCB	-28.80	±	5.57	-0.24	-0.29	-0.19	-0.40	-0.07
ral	15m	PB	-13.63	±	1.91	-0.15	-0.28	-0.04	-0.49	0.19
		SA	-16.30	\pm	0.94	0.00	-0.13	0.12	-0.40	0.34
Iarc		EG	-0.49	\pm	1.52	-0.08	-0.15	0.00	-0.29	0.16
Ч	15-	GCB	-18.65	±	7.43	-0.27	-0.32	-0.21	-0.45	-0.10
	20m	PB	-12.84	\pm	1.74	-0.19	-0.32	-0.10	-0.52	0.17
_		SA	-14.17	±	0.88	-0.03	-0.14	0.11	-0.39	0.34
		EG	7.96	\pm	2.49	-0.09	-0.16	-0.02	-0.31	0.11
	20-	GCB	-17.31	\pm	7.26	-0.30	-0.35	-0.24	-0.45	-0.13
	25m	PB	-9.58	\pm	1.98	-0.27	-0.38	-0.16	-0.61	0.07
		SA	-10.37	±	2.69	0.00	-0.14	0.12	-0.36	0.36
		EG	-12.91	±	12.65	-0.03	-0.11	0.05	-0.26	0.23
	5 10.00	GCB	-83.98	±	3.83	0.12	-0.01	0.22	-0.24	0.42
	5-10m	PB	-29.91	\pm	10.61	0.02	-0.11	0.15	-0.35	0.44
		SA	-22.96	±	29.68	-0.06	-0.19	0.06	-0.40	0.29
-		EG	-2.29	±	7.36	0.01	-0.08	0.14	-0.31	0.33
	10-	GCB	-38.71	\pm	7.09	0.20	0.06	0.39	-0.29	0.67
П	15m	PB	-33.27	\pm	5.44	0.07	-0.13	0.24	-0.51	0.60
cora		SA	-17.14	±	5.64	-0.01	-0.14	0.17	-0.47	0.43
oft		EG	-16.25	±	2.63	0.00	-0.08	0.10	-0.28	0.29
\mathbf{S}	15-	GCB	-4.77	\pm	13.71	0.22	0.12	0.35	-0.13	0.55
	20m	PB	-19.82	±	2.70	0.05	-0.10	0.23	-0.42	0.54
		SA	-32.38	±	4.19	-0.07	-0.20	0.09	-0.47	0.38
_		EG	-8.94	±	11.04	-0.10	-0.19	-0.02	-0.36	0.19
	20-	GCB	-20.66	\pm	9.09	-0.01	-0.10	0.11	-0.35	0.31
	25m	PB	-3.22	±	4.17	0.03	-0.12	0.21	-0.40	0.52
	<i></i>	SA	-21.05	±	3.16	-0.12	-0.31	-0.01	-0.53	0.31

		EG	4.44	\pm	2.91	0.06	-0.01	0.13	-0.13	0.25
	5 10m	GCB	13.65	±	7.01	0.15	0.07	0.24	-0.10	0.40
	J-10111	PB	7.12	\pm	4.03	0.10	-0.01	0.22	-0.25	0.43
		SA	11.97	±	2.99	0.02	-0.09	0.11	-0.28	0.32
		EG	8.67	\pm	2.29	-0.01	-0.08	0.11	-0.27	0.26
	10-	GCB	6.13	\pm	4.00	-0.04	-0.15	0.07	-0.36	0.32
	15m	PB	13.74	\pm	7.13	0.04	-0.10	0.24	-0.44	0.51
A		SA	18.98	±	4.06	0.02	-0.15	0.15	-0.41	0.45
S		EG	3.83	±	2.14	0.02	-0.07	0.10	-0.24	0.27
	15-	GCB	-4.12	±	4.48	-0.04	-0.13	0.04	-0.31	0.24
	20m	PB	9.32	±	3.05	0.06	-0.09	0.21	-0.39	0.50
		SA	13.07	±	1.78	0.05	-0.08	0.21	-0.35	0.45
		EG	1.74	±	2.39	-0.01	-0.13	0.07	-0.29	0.28
	20-	GCB	3.33	\pm	9.56	-0.10	-0.24	0.02	-0.47	0.29
	25m	PB	-8.35	\pm	6.84	-0.01	-0.14	0.21	-0.49	0.51
		SA	7.69	±	6.27	0.06	-0.10	0.22	-0.40	0.51
		EG	11.60	±	5.26	-0.04	-0.10	0.01	-0.21	0.12
	5 10	GCB	19.40	\pm	3.49	-0.01	-0.06	0.03	-0.15	0.14
	5-10m	PB	10.12	±	2.25	0.00	-0.10	0.09	-0.28	0.29
		SA	12.12	±	3.73	0.04	-0.06	0.13	-0.24	0.31
		EG	18.31	±	12.13	-0.09	-0.17	0.00	-0.33	0.15
	10-	GCB	12.65	±	2.27	0.02	-0.06	0.09	-0.23	0.25
nent	15m	PB	12.39	±	4.49	-0.03	-0.17	0.11	-0.46	0.40
ven		SA	17.36	±	6.54	-0.06	-0.21	0.07	-0.45	0.38
f pa		EG	33.55	±	14.26	-0.19	-0.26	-0.11	-0.42	0.03
Ree	15-	GCB	14.34	±	4.11	-0.06	-0.12	0.00	-0.25	0.11
	20m	PB	7.47	±	2.45	0.01	-0.09	0.16	-0.38	0.37
		SA	13.12	±	6.12	-0.16	-0.30	-0.04	-0.52	0.24
		EG	65.27	\pm	3.67	-0.12	-0.19	-0.04	-0.34	0.11
	20-	GCB	4.78	\pm	2.45	-0.02	-0.07	0.05	-0.21	0.18
	25m	PB	8.50	±	3.82	0.12	0.01	0.30	-0.31	0.53
		SA	-0.80	±	2.19	-0.10	-0.26	0.01	-0.48	0.30
		EG	10.87	\pm	2.85	0.04	-0.03	0.14	-0.22	0.31
	5-10m	GCB	52.57	±	11.65	-0.10	-0.20	-0.03	-0.37	0.15
	J-10111	PB	25.22	±	5.20	-0.05	-0.18	0.13	-0.48	0.42
		SA	33.32	±	6.87	0.07	-0.04	0.24	-0.35	0.48
ac		EG	9.93	±	1.07	-0.07	-0.18	0.06	-0.43	0.31
hon	10-	GCB	52.63	±	23.85	-0.24	-0.36	-0.14	-0.58	0.11
$\mathbf{\overline{N}}$	15m	PB	23.32	±	9.03	-0.22	-0.41	0.02	-0.86	0.40
		SA	16.08	±	8.10	-0.04	-0.24	0.18	-0.64	0.54
	15	EG	0.64	±	4.89	0.08	-0.01	0.22	-0.24	0.44
	13- 20m	GCB	10.00	±	6.66	0.06	-0.06	0.15	-0.24	0.36
	- 5111	PB	10.82	±	4.40	-0.04	-0.22	0.18	-0.63	0.54

	SA	21.40	±	6.37	0.10	-0.12	0.30	-0.50	0.65
	EG	-0.54	±	3.23	0.05	-0.05	0.17	-0.24	0.44
20-	GCB	4.57	±	4.09	0.11	0.02	0.20	-0.24	0.36
25m	PB	5.63	\pm	4.24	-0.26	-0.47	-0.09	-0.63	0.54
	SA	11.97	±	5.51	0.09	-0.12	0.28	-0.50	0.65

			Change	in c	over	Repeated	50%		95%	
b)	Depth	Atoll	Mean ±	SE ((%)	effects	Lower CI	Upper CI	Lower CI	Upper CI
		EG	6.93	\pm	1.27	0.09	0.06	0.14	-0.03	0.22
	5 10m	GCB	-38.14	\pm	4.42	0.08	0.05	0.12	-0.02	0.18
	J-10111	PB	-15.83	\pm	1.66	0.13	0.07	0.19	-0.05	0.29
		SA	-10.89	±	1.98	-0.01	-0.09	0.07	-0.27	0.24
		EG	0.69	\pm	1.65	0.11	0.07	0.18	-0.06	0.28
	10-	GCB	-28.80	\pm	5.57	0.13	0.10	0.18	0.01	0.25
al	15m	PB	-13.63	\pm	1.91	0.14	0.07	0.23	-0.10	0.37
COI		SA	-16.30	\pm	0.94	0.07	-0.02	0.21	-0.27	0.40
Iard		EG	-0.49	\pm	1.52	0.09	0.03	0.15	-0.09	0.26
j.L.j	15-	GCB	-18.65	\pm	7.43	0.17	0.13	0.22	0.02	0.29
	20m	PB	-12.84	\pm	1.74	0.13	0.04	0.19	-0.11	0.36
_		SA	-14.17	\pm	0.88	0.02	-0.12	0.12	-0.33	0.38
		EG	7.96	\pm	2.49	0.11	0.06	0.17	-0.06	0.27
	20-	GCB	-17.31	\pm	7.26	0.14	0.09	0.17	0.01	0.25
	25m	PB	-9.58	\pm	1.98	0.19	0.11	0.27	-0.06	0.41
		SA	-10.37	\pm	2.69	0.11	0.01	0.23	-0.21	0.45
		EG	-12.91	±	12.65	-0.05	-0.11	0.04	-0.26	0.18
	5-10m	GCB	-83.98	\pm	3.83	-0.21	-0.32	-0.12	-0.48	0.09
	5 1011	PB	-29.91	\pm	10.61	-0.06	-0.18	0.03	-0.35	0.24
		SA	-22.96	\pm	29.68	-0.04	-0.17	0.07	-0.42	0.29
		EG	-2.29	\pm	7.36	0.07	-0.01	0.16	-0.17	0.34
	10-	GCB	-38.71	\pm	7.09	-0.05	-0.15	0.04	-0.33	0.24
al	15m	PB	-33.27	\pm	5.44	0.12	-0.04	0.20	-0.23	0.47
cor		SA	-17.14	\pm	5.64	0.02	-0.14	0.20	-0.46	0.52
Soft		EG	-16.25	\pm	2.63	-0.01	-0.09	0.06	-0.23	0.21
	15-	GCB	-4.77	\pm	13.71	-0.10	-0.20	-0.04	-0.33	0.16
	20m	PB	-19.82	\pm	2.70	-0.07	-0.18	0.03	-0.38	0.24
		SA	-32.38	\pm	4.19	0.07	-0.10	0.20	-0.36	0.52
		EG	-8.94	\pm	11.04	-0.07	-0.16	-0.01	-0.30	0.14
	20-	GCB	-20.66	±	9.09	-0.19	-0.26	-0.11	-0.42	0.06
	25m	PB	-3.22	±	4.17	-0.10	-0.21	0.00	-0.40	0.21
		SA	-21.05	±	3.16	-0.05	-0.19	0.12	-0.49	0.43

5-10m GCB 13.65 ± 7.01 -0.01 -0.07 0.04 -0.18 0.17 V0 BB 7.12 ± 4.03 -0.11 -0.19 -0.02 -0.34 0.13 SA 11.97 ± 2.99 -0.05 -0.16 0.06 -0.07 -0.22 0.22 0.22 10- GCB 6.13 ± 4.00 0.02 -0.06 0.10 -0.22 0.22 0.22 15- GCB 4.12 ± 4.00 -0.07 -0.24 0.06 -0.21 0.16 20m BB 9.32 ± 3.05 -0.09 -0.21 0.00 -0.40 0.22 20- CCB 3.33 ± 9.56 0.10 0.02 0.01 -0.42 0.42 20- CB 10.0 ± 5.26 -0.01 -0.01 0.23 -0.44 0.54 20- PB 8.35 ± 6.			EG	4.44	\pm	2.91	0.00	-0.06	0.05	-0.16	0.17
PB 7.12 ± 4.03 -0.11 -0.19 -0.02 -0.34 0.13 SA 11.97 ± 2.99 -0.05 -0.16 0.06 -0.37 0.27 EG 8.67 ± 2.29 -0.05 -0.16 0.06 -0.022 0.22 10- DCGB 6.13 ± 4.00 0.02 -0.06 -0.49 0.16 15m PB 13.74 ± 7.13 -0.19 -0.29 -0.06 -0.49 0.16 SA 18.98 ± 4.06 -0.07 -0.24 0.06 -0.21 0.00 -0.40 0.22 20m PB 9.32 ± 3.05 -0.07 -0.13 0.00 -0.40 0.22 20m GCB 3.33 ± 9.56 0.10 0.02 0.20 -0.17 0.38 21m EG 11.60 ± 5.26 -0.10 0.02 -0.13 0.13		5-10m	GCB	13.65	\pm	7.01	-0.01	-0.07	0.04	-0.18	0.17
No. SA 11.97 ± 2.99 -0.05 -0.16 0.06 -0.37 0.27 ID- 15m GCB 6.13 ± 2.00 -0.08 0.07 -0.22 0.22 15m GCB 6.13 ± 4.00 0.02 -0.06 0.049 0.102 15m GCB 3.83 ± 2.14 0.00 -0.08 0.06 -0.21 0.19 15m GCB 3.12 ± 4.48 -0.07 -0.13 0.00 -0.44 0.16 20m PB 9.32 ± 3.05 -0.09 -0.01 0.01 -0.42 0.42 20- GCB 3.33 ± 9.56 0.10 0.02 0.01 -0.17 0.38 20- GCB 1.74 ± 2.39 0.04 -0.10 0.23 -0.14 0.33 1.13 0.13 0.13 0.13 0.13 0.13 0.13 0.13 0.15		J-10111	PB	7.12	\pm	4.03	-0.11	-0.19	-0.02	-0.34	0.13
Model EG 8.67 ± 2.29 0.00 -0.08 0.07 -0.22 0.22 Model RG 1.37 ± 7.13 0.019 -0.06 0.10 -0.22 0.25 No 1.87 ± 7.13 0.19 -0.02 -0.06 -0.49 0.16 15- EG 3.83 ± 2.14 0.00 -0.08 0.06 -0.21 0.19 15- GCB -4.12 ± 4.48 -0.07 -0.13 0.00 -0.24 0.16 0.22 20- RG 3.33 ± 2.178 0.02 -0.11 0.17 -0.42 0.42 20- RG 3.33 ± 2.56 0.10 0.02 0.01 0.17 0.38 20- RG 3.35 ± 6.54 0.10 0.02 0.17 0.38 20- RG 1.60 ± 5.26 0.01 0.02 0.13			SA	11.97	±	2.99	-0.05	-0.16	0.06	-0.37	0.27
10- 15m GCB 6.13 ± 4.00 0.02 -0.06 0.10 -0.22 0.25 V0 SA 13.74 ± 7.13 0.19 -0.29 -0.06 -0.49 0.16 SA 18.98 ± 2.14 0.00 -0.024 0.06 -0.21 0.01 15- 20m GCB 3.13 ± 2.14 0.00 -0.013 0.00 -0.24 0.16 20m BB 9.32 ± 3.05 -0.09 -0.21 0.00 -0.42 0.42 20- 20m PB 9.32 ± 3.05 0.02 -0.01 0.02 0.01 0.02 0.01 0.22 20- 25m PB 3.33 ± 9.56 0.10 0.02 0.01 0.04 0.02 0.01 0.04 0.23 0.44 0.51 200 CB 3.33 ± 9.56 0.01 -0.02 0.01 0.02 0.02 0.13			EG	8.67	±	2.29	0.00	-0.08	0.07	-0.22	0.22
		10-	GCB	6.13	±	4.00	0.02	-0.06	0.10	-0.22	0.25
SA 18.98 ± 4.06 -0.07 -0.24 0.06 -0.53 0.39 15- 20m EG 3.83 ± 2.14 0.00 -0.08 0.06 -0.21 0.19 20m PB 9.32 ± 3.05 -0.09 -0.21 0.00 -0.40 0.22 SA 13.07 ± 1.78 0.02 -0.11 0.17 -0.422 0.42 20- 20- 25m GCB 3.33 ± 9.56 0.10 0.02 0.01 -0.21 0.04 20- 25m GCB 3.33 ± 9.56 0.10 0.02 -0.01 -0.47 0.23 SA 7.69 ± 6.27 0.06 -0.10 0.23 -0.44 0.54 5-10m PB 10.12 ± 5.26 -0.01 -0.07 0.02 -0.13 0.13 10- BCB 18.31 ± 12.13 -0.05 -0.12 0.01 -0.24		15m	PB	13.74	±	7.13	-0.19	-0.29	-0.06	-0.49	0.16
S EG 3.83 ± 2.14 0.00 -0.08 0.06 -0.21 0.19 15- 20m GCB -4.12 ± 4.48 -0.07 -0.13 0.00 -0.24 0.16 20m PB 9.32 ± 3.05 -0.09 -0.21 0.00 -0.40 0.22 SA 13.07 ± 1.78 0.02 -0.11 0.17 -0.42 0.42 20- GCB 3.33 ± 9.56 0.10 0.02 0.01 -0.47 0.23 SA 7.69 ± 6.27 0.06 -0.10 0.23 -0.44 0.54 BA 7.69 ± 6.27 0.06 -0.10 0.02 -0.13 0.13 SA 7.69 ± 6.27 0.06 -0.12 0.01 -0.42 0.14 10.12 ± 2.25 -0.06 -0.12 0.01 -0.26 0.14 10- GCB	CA		SA	18.98	±	4.06	-0.07	-0.24	0.06	-0.53	0.39
15- 20m GCB PB 9.32 ± 4.48 -0.07 -0.13 0.00 -0.24 0.16 20m PB 9.32 ± 3.05 -0.09 -0.21 0.00 -0.40 0.22 SA 13.07 ± 1.78 0.02 -0.11 0.17 -0.42 0.42 20- 25m GCB 3.33 ± 9.56 0.10 0.02 0.20 -0.17 0.38 20- 25m GCB 1.74 ± 2.39 0.04 -0.05 0.11 -0.22 0.23 SA 7.69 ± 6.27 0.06 -0.10 0.23 -0.44 0.54 PB 10.12 ± 2.25 -0.06 -0.12 0.01 -0.24 0.14 10- 15m GCB 19.40 ± 3.49 0.04 0.01 0.02 -0.22 0.06 0.14 11 0.12 0.02 -0.20 0.01 0.01 0.02 0.02	ŭ		EG	3.83	\pm	2.14	0.00	-0.08	0.06	-0.21	0.19
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		15-	GCB	-4.12	±	4.48	-0.07	-0.13	0.00	-0.24	0.16
		20m	PB	9.32	\pm	3.05	-0.09	-0.21	0.00	-0.40	0.22
			SA	13.07	\pm	1.78	0.02	-0.11	0.17	-0.42	0.42
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			EG	1.74	\pm	2.39	0.04	-0.05	0.11	-0.22	0.25
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$		20-	GCB	3.33	\pm	9.56	0.10	0.02	0.20	-0.17	0.38
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		25m	PB	-8.35	\pm	6.84	-0.13	-0.25	-0.01	-0.47	0.23
$ \begin{tabular}{ c c c c c c c c c c c c c c c c c c c$			SA	7.69	±	6.27	0.06	-0.10	0.23	-0.44	0.54
5-10m GCB 19.40 ± 3.49 0.04 0.01 0.08 -0.08 0.15 PB 10.12 ± 2.25 -0.06 -0.12 0.01 -0.24 0.14 SA 12.12 ± 3.73 0.09 0.00 0.18 -0.17 0.38 10- GCB 12.65 ± 2.27 -0.01 -0.07 0.04 -0.19 0.17 PB 12.39 ± 4.49 0.00 -0.10 0.09 -0.30 0.27 SA 17.36 ± 6.54 -0.07 -0.22 0.06 -0.45 0.36 15- GCB 14.34 ± 4.11 0.06 0.02 0.10 -0.07 0.20 20- GCB 4.78 ± 2.45 -0.01 -0.12 0.05 -0.24 0.25 SA 13.12 ± 6.12 -0.13 -0.25 -0.01 -0.48 0.25			EG	11.60	\pm	5.26	-0.01	-0.07	0.02	-0.13	0.13
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		5 10m	GCB	19.40	\pm	3.49	0.04	0.01	0.08	-0.08	0.15
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		5-10111	PB	10.12	±	2.25	-0.06	-0.12	0.01	-0.24	0.14
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			SA	12.12	\pm	3.73	0.09	0.00	0.18	-0.17	0.38
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			EG	18.31	\pm	12.13	-0.05	-0.12	0.02	-0.26	0.14
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		10-	GCB	12.65	±	2.27	-0.01	-0.07	0.04	-0.19	0.17
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	nen	15m	PB	12.39	±	4.49	0.00	-0.10	0.09	-0.30	0.27
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Iver		SA	17.36	±	6.54	-0.07	-0.22	0.06	-0.45	0.36
$ \frac{9}{20} \frac{15}{20m} = \begin{array}{ccccccccccccccccccccccccccccccccccc$	f pa		EG	33.55	±	14.26	-0.04	-0.10	0.02	-0.22	0.14
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Ree	15-	GCB	14.34	\pm	4.11	0.06	0.02	0.10	-0.07	0.20
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		20m	PB	7.47	\pm	2.45	-0.01	-0.12	0.05	-0.24	0.25
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			SA	13.12	\pm	6.12	-0.13	-0.25	-0.01	-0.48	0.25
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			EG	65.27	\pm	3.67	0.14	0.07	0.19	-0.05	0.33
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		20-	GCB	4.78	\pm	2.45	0.04	0.01	0.09	-0.10	0.18
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		25m	PB	8.50	\pm	3.82	-0.06	-0.18	0.01	-0.33	0.23
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			SA	-0.80	±	2.19	0.21	0.08	0.33	-0.17	0.57
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			EG	10.87	\pm	2.85	-0.05	-0.14	0.01	-0.26	0.17
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		5-10m	GCB	52.57	\pm	11.65	-0.06	-0.12	0.00	-0.24	0.14
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		5 10111	PB	25.22	\pm	5.20	-0.09	-0.20	0.01	-0.40	0.21
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			SA	33.32	±	6.87	-0.01	-0.17	0.11	-0.42	0.40
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ge		EG	9.93	\pm	1.07	-0.10	-0.22	-0.01	-0.40	0.20
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	bon	10-	GCB	52.63	\pm	23.85	-0.10	-0.19	-0.03	-0.34	0.16
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	\mathbf{v}	15m	PB	23.32	\pm	9.03	-0.18	-0.32	-0.04	-0.57	0.23
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			SA	16.08	\pm	8.10	-0.08	-0.30	0.10	-0.67	0.50
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		15-	EG	0.64	\pm	4.89	-0.02	-0.10	0.09	-0.30	0.28
$PB 10.82 \pm 4.40 -0.17 -0.30 -0.03 -0.55 0.22$		20m	GCB	10.00	\pm	6.66	-0.09	-0.16	-0.01	-0.31	0.13
			PB	10.82	\pm	4.40	-0.17	-0.30	-0.03	-0.55	0.22

	SA	21.40	<u>+</u>	6.37	0.00	-0.18	0.19	-0.57	0.55	
	EG	-0.54	\pm	3.23	-0.01	-0.10	0.10	-0.30	0.28	
20-	GCB	4.57	\pm	4.09	-0.02	-0.10	0.03	-0.31	0.13	
25m	PB	5.63	\pm	4.24	-0.02	-0.15	0.10	-0.55	0.22	
	SA	11.97	±	5.51	0.06	-0.10	0.26	-0.57	0.55	



Atoll \circ EG \square GCB \diamond PB \triangle SA Heatwaves - pre \clubsuit post



Heatwaves - pre 🔶 post

Figure S1: Non-metric multi-dimensional scaling plots (nMDS) of benthic groups from 16 sites in the Chagos Archipelago, showing clustering of communities in 2013/14 (pre) and 2018/19 (post) following the 2015–2017 marine heatwaves across a) depth zones and b) atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA), based on Bray-Curtis dissimilarities of square-root transformed data. Ellipses represent dispersion of pre (grey lines) and post (black lines) marine heatwaves communities from centroids at 95% confidence intervals. Vectors show benthic groups that significantly contributed to the patterns on the ordination, arrows show the direction of the gradient, and the length of the vectors are proportional to the correlations between the benthic group and the ordination.



Figure S2: Percentage cover of benthic groups pre (grey) and post (black) 2015–2017 marine heatwaves across depth zones at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).



Figure S3: Standardised effects of depth zones on change in benthic groups cover following the 2015–2017 marine heatwaves at atolls Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points indicate median estimates and bars represent 50% and 95% credible intervals. Strong and weak evidence of change in benthic cover are interpreted when 95% and 50% of the intervals do not intercept zero, respectively. Note different x-axis across benthic groups.

Appendix C - Supplementary materials for Chapter 4: Effects of depth on coral carbonate production on remote reefs

Atoll	Site	Lat	Long
	North	-6.636	71.318
FG	Middle	-6.635	71.363
ĽŪ	Lubine	-6.643	71.358
	Tattamucca	-6.694	71.381
	Middle Brother Channel	-6.157	71.511
CCP	Middle Brother Drop	-6.149	71.517
UCD	North Brother	-6.139	71.507
	South Brother	-6.177	71.540
	Ile Diamant	-5.235	71.771
DD	Petite Ile Coquillage	-5.348	71.969
ГD	Ile Poule	-5.398	71.749
	Ile Yeye	-5.252	71.975
	Ile Passe	-5.286	72.259
S۸	Ile Anglaise South Tip	-5.344	72.202
SA	Ile Anglaise Middle	-5.332	72.219
	Takamaka	-5.347	72.269

Table S1: List of surveyed sites at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

Table S2: List of prior specifications for linear regression models of coral carbonate budget, coral G, and coral cover across depth, atolls, and method. Both coral G and coral cover were log transformed. Note that the brms package automatically truncates the prior specification for σ and allow only positive values

Model	Prior specifications
Coral $G_i \sim Normal (\mu_i, \sigma_i)$ $\mu_i = \beta_{j[i]} + \beta_1(depth \ x \ atoll \ x \ method) + \sigma_{s[i]}$	$\beta_{j[i]} \sim N (1.2, 0.8)$ [depth-specific intercepts: for each depth zone j in $(1j)$] $\beta_1 \sim N (1.2, 0.8)$ $\sigma_{s[i]} \sim N (0, 2.5)$ [Offsets for grouping variable: site, s, nested in atoll]
Coral cover _i ~ Normal (μ_i, σ_i) $\mu_i = \beta_{j[i]} + \beta_1(depth \ x \ atoll \ x \ method) + \sigma_{s[i]}$	$\begin{aligned} \beta_{j[i]} &\sim N \ (2.9, \ 0.7) \\ \beta_1 &\sim N \ (2.9, \ 0.7) \\ \sigma_{s[i]} &\sim N \ (0, \ 2.5) \end{aligned}$

Table S3: Pairwise comparisons showing significant difference in permutational analysis of variance (PERMANOVA) among atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

Pairwise comparisons	F value	p value
EG vs GCB	3.916	0.018
EG vs PB	4.045	0.012
EG vs SA	2.980	0.048
GCB vs SA	3.336	0.012

Table S4: Coral genera combinations characterising a) shallow (10 m) and deep (17.5 m) reefs and b) atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). 'A' indicates the specificity of coral genera, i.e., the probability of finding coral genera as indicators of depth or atoll groups, 'B' represents the fidelity of coral genera, i.e., the probability of finding coral genera as indicators of the samples collected within the respective depth and atoll groups, and 'SqrtIV' shows the square-root of the indicator value index. The lower and upper confidence intervals (CI) were calculated using bootstrapping (n=10,000).

a) Depth	Genera	А	Lower	Upper	В	Lower	Upper	Sqrt	Lower	Upper	p-
/ 1			CI	CI		CI	CI	IV	CI	CI	value
	Pocillopora+Acropora	0.600	0.476	0.716	0.813	0.689	0.918	0.698	0.595	0.786	0.0066
Shallow	Pocillopora+Acropora+Porites	0.600	0.476	0.716	0.813	0.689	0.918	0.698	0.595	0.786	0.0066
	Pavona+Montipora+Psammocora	0.848	0.663	0.965	0.333	0.205	0.469	0.532	0.389	0.649	0.0015
	Pavona+Montipora+Porites	0.628	0.465	0.773	0.750	0.622	0.868	0.687	0.565	0.789	0.0256
	Pavona+Montipora+Platygyra	0.724	0.519	0.880	0.333	0.208	0.475	0.491	0.343	0.620	0.015
	Pavona+Montipora+Favites	0.665	0.502	0.805	0.688	0.553	0.811	0.676	0.551	0.777	0.0086
	Pavona+Montipora+Other	0.694	0.525	0.827	0.708	0.578	0.833	0.701	0.575	0.798	0.0051
	Pavona+Psammocora	0.858	0.676	0.962	0.396	0.261	0.540	0.583	0.442	0.696	0.0018
	Pavona+Psammocora+Acropora	0.788	0.553	0.940	0.292	0.164	0.425	0.479	0.324	0.606	0.014
	Pavona+Psammocora+Porites	0.857	0.673	0.962	0.396	0.261	0.540	0.582	0.442	0.696	0.0019
Moderate	Pavona+Psammocora+Goniastrea	0.865	0.688	0.961	0.396	0.261	0.540	0.585	0.447	0.698	0.0017
	Pavona+Psammocora+Favites	0.853	0.669	0.973	0.375	0.244	0.518	0.566	0.424	0.682	0.001
	Pavona+Psammocora+Other	0.869	0.694	0.970	0.396	0.261	0.540	0.586	0.449	0.700	0.0015
	Pavona+Acropora+Porites	0.636	0.489	0.766	0.792	0.667	0.902	0.710	0.595	0.802	0.0084
	Pavona+Acropora+Platygyra	0.769	0.575	0.900	0.375	0.240	0.518	0.537	0.393	0.658	0.0047
	Pavona+Acropora+Goniastrea	0.633	0.483	0.764	0.771	0.643	0.886	0.699	0.580	0.793	0.0125
	Pavona+Acropora+Favites	0.721	0.579	0.833	0.729	0.596	0.849	0.725	0.613	0.815	0.0005
P P P P	Pavona+Acropora+Other	0.695	0.545	0.818	0.771	0.644	0.885	0.732	0.618	0.823	0.0009
	Pavona+Porites+Platygyra	0.759	0.571	0.894	0.417	0.280	0.561	0.562	0.420	0.682	0.0031
	Pavona+Porites+Goniastrea	0.700	0.558	0.815	0.896	0.804	0.978	0.792	0.693	0.869	0.0003
	Pavona+Porites+Favites	0.743	0.612	0.850	0.813	0.696	0.915	0.777	0.677	0.857	0.0003

Pavona+Porites+Other	0.720	0.570	0.841	0.875	0.775	0.961	0.794	0.689	0.873	0.0005
Pavona+Platygyra+Goniastrea	0.782	0.593	0.911	0.417	0.280	0.561	0.571	0.430	0.691	0.0021
Pavona+Platygyra+Favites	0.765	0.579	0.906	0.417	0.280	0.561	0.564	0.423	0.686	0.0028
Pavona+Platygyra+Other	0.752	0.562	0.901	0.396	0.262	0.538	0.546	0.404	0.669	0.0047
Pavona+Goniastrea+Favites	0.720	0.581	0.834	0.792	0.673	0.900	0.755	0.648	0.840	0.0004
Pavona+Goniastrea+Other	0.701	0.547	0.824	0.854	0.750	0.949	0.774	0.667	0.857	0.0014
Pavona+Favites+Other	0.739	0.600	0.851	0.792	0.674	0.898	0.765	0.659	0.849	0.0004
Montipora+Psammocora+Acropora	0.793	0.552	0.947	0.250	0.132	0.377	0.445	0.285	0.570	0.0141
Montipora+Psammocora+Porites	0.829	0.636	0.957	0.333	0.205	0.469	0.526	0.382	0.644	0.0019
Montipora+Psammocora+Goniastrea	0.829	0.636	0.957	0.333	0.205	0.469	0.526	0.382	0.644	0.0019
Montipora+Psammocora+Favites	0.864	0.687	0.973	0.333	0.205	0.469	0.537	0.395	0.653	0.0011
Montipora+Psammocora+Other	0.884	0.717	0.980	0.333	0.205	0.469	0.543	0.404	0.657	0.0005
Montipora+Acropora+Platygyra	0.716	0.500	0.876	0.292	0.170	0.429	0.457	0.305	0.588	0.0219
Montipora+Acropora+Other	0.623	0.464	0.756	0.667	0.529	0.795	0.644	0.517	0.746	0.0248
Montipora+Porites+Platygyra	0.726	0.522	0.880	0.333	0.208	0.475	0.492	0.344	0.620	0.0139
Montipora+Porites+Other	0.636	0.480	0.769	0.750	0.623	0.867	0.691	0.571	0.787	0.0129
Montipora+Platygyra+Goniastrea	0.739	0.538	0.893	0.333	0.208	0.475	0.496	0.349	0.624	0.0101
Montipora+Platygyra+Favites	0.746	0.548	0.900	0.333	0.208	0.475	0.499	0.353	0.627	0.0064
Montipora+Platygyra+Other	0.721	0.513	0.882	0.313	0.189	0.449	0.475	0.326	0.604	0.0169
Montipora+Goniastrea+Other	0.637	0.483	0.772	0.750	0.623	0.867	0.691	0.571	0.789	0.0128
Montipora+Favites+Other	0.645	0.477	0.783	0.667	0.532	0.792	0.655	0.530	0.757	0.0187
Psammocora+Acropora+Porites	0.795	0.574	0.937	0.292	0.164	0.425	0.481	0.327	0.607	0.0079
Psammocora+Acropora+Goniastrea	0.791	0.574	0.931	0.292	0.164	0.425	0.480	0.326	0.605	0.0084
Psammocora+Acropora+Favites	0.820	0.600	0.967	0.292	0.164	0.425	0.489	0.336	0.612	0.0066
Psammocora+Acropora+Other	0.875	0.694	0.972	0.292	0.164	0.425	0.505	0.358	0.623	0.0026
Psammocora+Porites+Goniastrea	0.878	0.721	0.963	0.396	0.261	0.540	0.590	0.455	0.700	0.0006
Psammocora+Porites+Favites	0.865	0.696	0.976	0.375	0.244	0.518	0.570	0.432	0.685	0.0005
Psammocora+Porites+Other	0.902	0.762	0.978	0.396	0.261	0.540	0.598	0.466	0.708	0.0003
Psammocora+Goniastrea+Favites	0.865	0.696	0.976	0.375	0.244	0.518	0.570	0.432	0.685	0.0005
Psammocora+Goniastrea+Other	0.894	0.748	0.976	0.396	0.261	0.540	0.595	0.462	0.706	0.0003

Psammocora+Favites+Other	0.869	0.685	0.983	0.375	0.244	0.518	0.571	0.432	0.688	0.0008
Psammocora+Other	0.902	0.762	0.978	0.396	0.261	0.540	0.598	0.466	0.708	0.0003
Acropora+Porites+Platygyra	0.761	0.578	0.891	0.375	0.240	0.518	0.534	0.391	0.655	0.0029
Acropora+Porites+Favites	0.609	0.465	0.738	0.729	0.596	0.849	0.667	0.548	0.764	0.0196
Acropora+Porites+Other	0.609	0.468	0.734	0.813	0.694	0.918	0.704	0.593	0.795	0.0162
Acropora+Platygyra+Goniastrea	0.801	0.613	0.919	0.375	0.240	0.518	0.548	0.404	0.665	0.0021
Acropora+Platygyra+Favites	0.745	0.553	0.893	0.375	0.240	0.518	0.528	0.383	0.651	0.005
Acropora+Platygyra+Other	0.749	0.555	0.898	0.354	0.225	0.500	0.515	0.371	0.641	0.0056
Acropora+Goniastrea+Other	0.608	0.469	0.732	0.792	0.673	0.900	0.694	0.583	0.788	0.0171
Acropora+Favites+Other	0.681	0.533	0.800	0.708	0.574	0.830	0.694	0.577	0.789	0.0019
Porites+Platygyra+Goniastrea	0.778	0.599	0.905	0.417	0.280	0.561	0.569	0.428	0.688	0.0018
Porites+Platygyra+Favites	0.739	0.555	0.888	0.417	0.280	0.561	0.555	0.412	0.678	0.003
Porites+Platygyra+Other	0.760	0.573	0.903	0.396	0.262	0.538	0.548	0.406	0.671	0.0033
Porites+Goniastrea+Favites	0.630	0.487	0.762	0.813	0.698	0.917	0.715	0.607	0.808	0.0066
Porites+Goniastrea+Other	0.668	0.535	0.782	0.896	0.804	0.978	0.774	0.678	0.850	0.0007
Porites+Favites+Other	0.687	0.548	0.803	0.792	0.674	0.898	0.737	0.632	0.824	0.0004
Platygyra+Goniastrea+Favites	0.753	0.570	0.897	0.417	0.280	0.561	0.560	0.418	0.682	0.0027
Platygyra+Goniastrea+Other	0.790	0.608	0.923	0.396	0.262	0.538	0.559	0.418	0.680	0.0015
Platygyra+Favites+Other	0.770	0.581	0.917	0.396	0.262	0.538	0.552	0.410	0.674	0.0022
Goniastrea+Favites+Other	0.656	0.511	0.785	0.771	0.651	0.884	0.711	0.600	0.805	0.0038
Pocillopora+Psammocora	0.777	0.497	0.932	0.250	0.130	0.381	0.441	0.271	0.571	0.0324
Pavona	0.686	0.535	0.815	0.917	0.830	0.981	0.793	0.689	0.875	0.001
Pavona+Montipora	0.624	0.461	0.768	0.750	0.622	0.868	0.684	0.561	0.786	0.0299
Pavona+Psammocora	0.858	0.676	0.962	0.396	0.261	0.540	0.583	0.442	0.696	0.0018
Pavona+Acropora	0.639	0.493	0.768	0.792	0.667	0.902	0.711	0.598	0.803	0.0073
Pavona+Porites	0.682	0.532	0.811	0.917	0.830	0.981	0.791	0.687	0.873	0.0015
Pavona+Platygyra	0.776	0.590	0.903	0.417	0.280	0.561	0.569	0.428	0.687	0.0024
Pavona+Goniastrea	0.706	0.565	0.818	0.896	0.804	0.978	0.795	0.697	0.871	0.0003
Pavona+Favites	0.747	0.616	0.851	0.813	0.696	0.915	0.779	0.679	0.858	0.0003
Montipora+Psammocora	0.829	0.636	0.957	0.333	0.205	0.469	0.526	0.382	0.644	0.0019

Montipora+Platygyra	0.726	0.522	0.880	0.333	0.208	0.475	0.492	0.344	0.620	0.0139
<i>Pavona+Other</i>	0.723	0.575	0.842	0.875	0.775	0.961	0.795	0.692	0.874	0.0004
Montipora+Psammocora	0.829	0.636	0.957	0.333	0.205	0.469	0.526	0.382	0.644	0.0019
Montipora+Other	0.638	0.485	0.770	0.771	0.648	0.884	0.702	0.582	0.796	0.011
Psammocora	0.876	0.717	0.964	0.396	0.261	0.540	0.589	0.453	0.700	0.0007
Psammocora+Acropora	0.797	0.579	0.937	0.292	0.164	0.425	0.482	0.328	0.608	0.0075
Psammocora+Porites	0.875	0.715	0.963	0.396	0.261	0.540	0.588	0.453	0.700	0.0008
Psammocora+Favites	0.865	0.696	0.976	0.375	0.244	0.518	0.570	0.432	0.685	0.0005
Acropora+Platygyra	0.793	0.606	0.910	0.375	0.240	0.518	0.545	0.401	0.663	0.0022
Acropora+Favites	0.646	0.490	0.774	0.729	0.596	0.849	0.686	0.562	0.783	0.01
Porites+Platygyra	0.772	0.593	0.897	0.417	0.280	0.561	0.567	0.427	0.685	0.0019
Porites+Goniastrea	0.622	0.494	0.736	0.958	0.895	1.000	0.772	0.683	0.844	0.0009
Porites+Favites	0.676	0.518	0.806	0.833	0.723	0.932	0.751	0.637	0.839	0.0024
Platygyra	0.801	0.622	0.914	0.417	0.280	0.561	0.578	0.436	0.693	0.0015
Platygyra+Goniastrea	0.809	0.631	0.922	0.417	0.280	0.561	0.581	0.440	0.695	0.0015
Platygyra+Favites	0.753	0.570	0.897	0.417	0.280	0.561	0.560	0.418	0.682	0.0027
Platygyra+Other	0.765	0.579	0.906	0.396	0.262	0.538	0.550	0.408	0.672	0.0031
Goniastrea	0.619	0.487	0.734	0.979	0.932	1.000	0.778	0.688	0.850	0.0021
Goniastrea+Favites	0.630	0.490	0.761	0.813	0.698	0.917	0.716	0.608	0.808	0.0062
Favites	0.698	0.542	0.820	0.833	0.723	0.932	0.762	0.650	0.848	0.0013
Favites+Other	0.704	0.564	0.819	0.792	0.674	0.898	0.747	0.640	0.832	0.0003
Other	0.759	0.611	0.859	0.938	0.861	1.000	0.844	0.750	0.907	0.0002

b) Atoll	Genera	А	Lower CI	Upper CI	В	Lower CI	Upper CI	Sqrt IV	Lower CI	Upper CI	p- value
EG	Acropora+Favites+Other	0.363	0.184	0.535	0.750	0.560	0.913	0.522	0.347	0.664	0.038
EO	Acropora+Other	0.353	0.210	0.500	0.875	0.722	1.000	0.556	0.411	0.677	0.021
CCP	Pocillopora+Pavona+Favites	0.441	0.213	0.632	0.458	0.261	0.667	0.449	0.250	0.609	0.011
UCB	Montipora+Platygyra+ Other	0.452	0.211	0.674	0.417	0.217	0.625	0.434	0.229	0.606	0.022

	Pocillopora+Psammocora	0.573	0.191	0.803	0.292	0.115	0.481	0.409	0.166	0.589	0.017
PB	Pocillopora+Psammocora+Porites	0.573	0.191	0.803	0.292	0.115	0.481	0.409	0.166	0.589	0.017
	Pocillopora+Psammocora+Goniastrea	0.564	0.178	0.799	0.292	0.115	0.481	0.406	0.161	0.586	0.020
	Acropora+Platygyra	0.439	0.139	0.667	0.333	0.148	0.536	0.382	0.156	0.558	0.049
SA	Acropora+Platygyra+Goniastrea	0.466	0.153	0.690	0.333	0.148	0.536	0.394	0.164	0.571	0.033
	Platygyra+Goniastrea	0.447	0.144	0.672	0.333	0.148	0.536	0.386	0.158	0.564	0.043

Table S5: Percentage cover (%) and proportional contribution of morphotypes to coral carbonate budget (prop coral G %) between *CoralNet* and *ReefBudget* between shallow (10 m) and moderate reefs (17.5 m) across atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Enc/Fol: Encrusting/Foliose, Branch Acro: Branching Acropora, Massive Por: Massive *Porites*, Tab Acro: Tabular *Acropora*.

A toll	MCG		Cover (%)			Prop Coral G (%)													
Aton	MCG			Cove	[(%)					Cora	lNet					ReefE	Budget		
		1	0m		17	7.5n	1	1	l0m		17	7.5n	1	1	l0m		1′	7.5n	1
	Total	28.75	\pm	1.41	20.75	±	1.02												
	Branching	0.56	±	0.18	0.78	\pm	0.61	1.41	\pm	0.50	1.84	\pm	1.19	2.44	\pm	1.34	3.40	\pm	1.03
	Enc/Fol	5.33	±	1.02	9.33	\pm	1.40	10.09	\pm	2.00	31.62	\pm	5.32	35.37	\pm	5.62	12.51	\pm	2.34
EG	Massive	2.67	±	0.65	3.00	±	0.63	11.32	±	2.31	16.04	±	3.93	10.33	±	2.80	1.22	±	0.31
	Branch Acro	14.06	±	3.57	4.28	±	1.11	34.86	±	5.82	18.44	±	3.62	30.37	±	7.47	46.24	±	7.65
	Massive Por	8.00	±	2.04	3.67	±	1.37	28.18	±	6.23	15.70	±	4.16	15.69	±	4.27	27.09	±	7.36
	Tab Acro	2.33	±	1.32	0.33	±	0.15	4.97	±	2.44	1.25	±	0.56	1.86	±	1.32	7.65	±	3.46
	Total	13.18	±	0.72	9.50	±	0.52												
	Branching	0.56	±	0.21	1.06	±	0.59	2.84	±	1.14	5.18	±	2.46	15.43	±	7.24	11.66	±	2.99
	Enc/Fol	4.22	±	0.92	5.17	±	0.71	19.34	±	5.24	23.66	±	3.21	38.83	±	5.25	31.23	±	4.47
GCB	Massive	2.22	±	0.61	3.50	±	1.00	15.91	±	3.65	23.73	±	5.13	9.46	±	2.66	4.62	±	1.86
	Branch Acro	1.11	±	0.35	0.44	±	0.15	8.77	±	2.76	2.93	±	0.98	7.92	±	3.18	24.08	±	6.16
	Massive Por	3.11	±	0.94	3.06	±	1.08	20.10	±	4.50	12.29	±	2.79	22.13	±	3.87	21.40	±	3.92
	Tab Acro	0.17	±	0.12	0.06	±	0.06	1.37	±	0.95	0.55	±	0.55	0.00	±	0.00	2.36	±	1.59

	Total	21.83	\pm	1.88	15.78	\pm	1.36												
	Branching	2.11	±	0.65	0.44	\pm	0.15	8.87	\pm	2.50	3.65	\pm	1.37	11.49	\pm	3.80	18.70	\pm	5.61
	Enc/Fol	6.67	±	1.09	8.61	\pm	2.09	14.99	\pm	2.92	28.26	±	3.82	29.78	±	4.34	18.14	±	3.77
PB	Massive	3.28	±	0.79	2.11	\pm	0.54	16.03	\pm	3.75	11.11	±	2.39	8.63	±	2.61	2.11	\pm	0.72
	Branch Acro	4.22	±	1.68	2.17	\pm	1.09	14.52	\pm	3.86	9.73	±	2.88	20.17	±	6.14	27.46	±	6.61
	Massive Por	5.67	±	0.89	3.44	\pm	0.90	26.72	\pm	3.18	20.54	±	3.69	21.79	±	3.71	20.56	±	4.28
	Tab Acro	0.78	±	0.33	0.22	±	0.22	4.80	±	1.75	1.38	±	1.38	1.60	±	0.96	5.09	±	1.97
	Total	26.63	±	1.35	19.25	\pm	0.97												
	Branching	2.44	±	0.49	1.11	\pm	0.46	11.60	\pm	2.93	4.10	±	1.72	10.63	±	2.92	17.40	±	4.55
	Enc/Fol	7.72	±	0.85	8.78	±	1.10	21.15	±	2.72	31.57	±	4.55	30.87	±	4.01	17.94	±	3.59
SA	Massive	1.33	±	0.22	1.78	\pm	0.39	8.82	\pm	1.46	11.19	±	2.09	2.97	±	0.57	2.24	±	0.81
	Branch Acro	4.61	±	0.91	2.72	\pm	1.20	14.91	\pm	2.35	9.83	±	2.79	22.03	±	5.41	21.53	±	4.18
	Massive Por	3.50	±	0.69	3.78	±	0.95	16.88	±	3.81	22.48	±	4.92	17.95	±	3.52	10.66	±	3.55
	Tab Acro	9.44	±	3.41	2.22	\pm	1.28	22.04	\pm	6.09	8.16	±	3.46	10.56	±	3.40	28.13	±	7.07

Table S6: Abundance and mean size of all coral colonies between shallow (10 m) and moderate (17.5 m) reefs across atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). N – total number of colonies, SD- standard deviation, SE – standard error.

Depth	Atoll	Ν	Mea	n±	SE	SD	Skew
	EG	680	18.88	±	0.79	20.58	1.08
10m	GCB	401	10.72	±	0.50	10.03	0.98
10111	PB	706	12.20	±	0.58	15.54	1.02
	SA	698	15.32	±	0.68	17.89	1.27
	EG	626	10.83	±	0.52	13.11	0.92
17.5m	GCB	466	10.20	±	0.54	11.66	1.03
17.5m	PB	589	10.09	±	0.48	11.55	1.05
	SA	692	11.09	±	0.51	13.46	1.03

Table S7: Abundance and mean size of coral morphotypes between shallow (10 m) and moderate (17.5 m) reefs across atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). N – total number of colonies, SD- standard deviation, SE – standard error, Enc/Fol: Encrusting/Foliose, Branch Acro: Branching Acropora, Massive Por: Massive *Porites*, Tab Acro: Tabular *Acropora*.

		10 mNMean + SESDMaxSke									17.	5 m			
Atoll	Morphotype	Ν	Mea	un +	SE	SD	Max	Skew	Ν	Mea	n + 1	SE	SD	Max	Skew
	Branching	13	26.85	\pm	4.35	15.70	56.19	1.42	14	15.23	\pm	5.65	21.15	83.05	0.80
	Enc/Fol	205	6.30	\pm	0.41	5.92	43.35	0.91	346	6.37	±	0.33	6.16	56.15	0.83
FG	Massive	46	9.01	\pm	0.99	6.70	32.32	0.50	77	11.28	±	0.97	8.53	47.69	0.70
ĽŪ	Massive Por	174	19.36	\pm	1.40	18.45	102.55	0.91	96	16.04	±	1.27	12.40	61.15	0.76
	Branch Acro	211	30.43	\pm	1.60	23.23	113.50	1.09	80	22.67	±	2.68	23.97	127.88	1.00
	Tab Acro	27	36.00	<u>+</u>	6.39	33.20	99.65	0.97	5	20.85	±	7.24	16.20	47.92	0.86
	Branching	13	31.43	\pm	4.79	17.28	64.74	0.37	81	6.62	\pm	1.14	10.23	52.75	0.92
	Enc/Fol	220	6.68	±	0.33	4.92	26.82	0.95	227	7.68	\pm	0.47	7.07	67.62	0.92
CCP	Massive	40	8.77	\pm	1.06	6.72	35.94	0.69	65	10.74	\pm	0.92	7.43	42.62	1.06
UCD	Massive Por	82	15.45	\pm	1.35	12.23	65.05	0.86	76	18.69	±	2.13	18.55	93.52	1.06
	Branch Acro	44	17.05	±	1.46	9.66	43.45	0.33	13	23.84	\pm	4.36	15.73	69.87	0.54
	Tab Acro	2	26.91	±	2.80	3.97	29.72	0.00	25	23.61	±	3.21	16.04	76.55	0.26
	Branching	41	30.69	\pm	3.12	19.98	75.02	0.89	321	5.49	±	0.35	6.30	81.94	0.64
	Enc/Fol	294	5.55	\pm	0.28	4.72	28.74	1.07	78	11.10	±	0.90	7.99	37.41	0.93
DD	Massive	83	10.10	\pm	0.88	8.04	51.98	0.80	102	14.72	±	1.25	12.65	70.82	0.85
ГD	Massive Por	175	12.12	\pm	0.92	12.17	90.60	1.05	48	21.33	±	2.76	19.09	113.87	1.15
	Branch Acro	94	26.63	\pm	2.77	26.85	168.00	0.81	3	20.80	±	8.36	14.48	36.61	0.67
	Tab Acro	14	16.30	\pm	3.44	12.88	49.99	1.16	40	18.68	±	1.86	11.77	49.55	0.64
	Branching	51	32.36	±	2.53	18.10	84.89	0.21	380	5.70	±	0.27	5.20	38.82	0.90
	Enc/Fol	319	5.70	\pm	0.28	5.02	58.14	0.72	47	9.92	\pm	1.46	9.99	61.89	0.89
с л	Massive	43	8.49	\pm	0.75	4.93	24.11	0.45	99	14.29	±	1.32	13.11	65.75	1.06
SA	Massive Por	84	17.23	\pm	1.99	18.21	81.15	1.29	71	27.61	±	2.85	24.02	103.81	0.99
	Branch Acro	86	24.80	±	2.25	20.83	96.43	1.10	31	21.39	±	3.06	17.06	70.32	0.91
	Tab Acro	108	29.99	±	2.18	22.69	93.74	0.97	40	18.68	±	1.86	11.77	49.55	0.64

Table S8: Percentage change (PCchange) in abundance of a) all coral colonies and b) different coral morphotypes relative to shallow reefs, separated in 3 size classes: small – representing first quintile, medium – second to fourth quintile and large: fifth quintile of colony size frequency distribution at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).

a) Atoll	Rin	Abundance on Abu shallow reefs mor	Abundance on	PCchange	66 %	6 CI	95 %	6 CI
a) Atom	DIII	shallow reefs	moderate reefs	PCchange 28.814 -15.345 -16.568 34.525 6.849 23.355 -32.298 -9.851 -27.573 11.273 -5.660 -12.230	Lower	Upper	Lower	Upper
	small	113	145	28.814	10.744	41.441	0.794	62.376
EG	medium	396	334	-15.345	-21.340	-9.138	-27.778	-3.593
	large	167	139	-16.568	-25.466	-7.843	-36.158	3.497
	small	68	93	34.525	12.500	53.968	1.190	83.929
GCB	medium	248	265	6.849	-3.213	13.750	-9.441	27.556
	large	85	104	23.355	4.255	38.462	-8.163	61.111
	small	153	104	-32.298	-40.136	-24.306	-48.889	-15.714
PB	medium	428	386	-9.851	-16.055	-4.009	-21.322	4.010
	large	120	87	-27.573	-38.519	-20.472	-44.444	-4.000
	small	134	151	11.273	0.637	26.190	-11.184	40.909
SA	medium	419	396	-5.660	-12.273	0.000	-18.122	8.462
	large	138	121	-12.230	-23.404	-3.788	-34.641	8.264

b)				Abundance on		66 9	% CI	95 %	CI
U) Mornhotyne	Atoll	Bin	Abundance on	moderate	PCchange				
Worphotype			shallow reefs	reefs		Lower	Upper	Lower	Upper
		small	0	5	0.000	0.000	0.000	0.000	0.000
	EG	medium	8	8	0.000	-50.000	33.333	-88.889	140.000
		large	5	1	-83.333	-100.000	-75.000	-100.000	-25.636
		small	0	49	0.000	0.000	0.000	0.000	0.000
Branching	GCB	medium	8	27	241.429	85.714	333.333	20.000	675.000
		large	5	5	0.000	-63.636	50.000	-100.000	221.722
		small	0	0	0.000	0.000	0.000	0.000	0.000
	PB	medium	26	22	-15.625	-46.667	0.000	-56.250	43.478
		large	15	3	-81.534	-94.444	-73.333	-100.000	-57.143

		small	0	2	0.000	0.000	0.000	0.000	0.000
	SA	medium	34	33	-2.667	-25.000	17.241	-43.902	46.667
		large	17	5	-70.588	-83.333	-55.556	-96.667	-37.500
		small	38	84	120.227	80.435	161.905	41.667	222.581
	EG	medium	122	180	47.236	28.099	60.684	11.111	80.952
		large	45	82	82.222	47.059	111.111	14.035	150.000
		small	31	24	-22.540	-46.154	-6.897	-56.250	22.727
	GCB	medium	130	138	6.299	-7.576	17.544	-16.352	37.398
Encrusting/		large	59	65	11.111	-8.475	29.091	-23.636	52.500
Foliose		small	63	65	3.419	-16.418	20.000	-29.333	43.750
	PB	medium	182	216	19.022	6.667	28.931	-5.102	41.212
	_	large	49	40	-18.750	-36.066	-4.082	-50.000	21.053
		small	68	90	32.857	12.162	50.980	-6.173	76.364
	SA	medium	199	219	10.025	0.441	21.320	-10.638	31.902
		large	52	71	36.118	11.667	56.863	-4.348	90.476
		small	15	13	-15.192	-50.000	8.333	-76.471	66.667
	EG	medium	23	42	80.952	31.818	115.789	6.061	191.667
		large	8	22	178.889	53.846	250.000	6.250	550.000
		small	10	9	-9.091	-50.000	25.000	-80.000	100.000
	GCB	medium	25	41	63.636	24.138	100.000	-9.302	160.000
Maggino		large	5	15	200.000	28.571	300.000	-33.333	795.434
Wassive		small	15	12	-18.750	-52.941	0.000	-72.222	62.500
	PB	medium	53	47	-11.342	-35.294	0.000	-43.077	26.667
		large	15	19	26.667	-15.000	66.667	-45.455	144.444
		small	12	10	-16.667	-61.538	0.000	-76.190	80.000
	SA	medium	26	30	16.667	-16.667	40.000	-40.000	88.235
		large	5	7	40.000	-40.000	100.000	-100.000	330.137
		small	29	18	-37.037	-62.069	-25.806	-73.077	0.000
	EG	medium	101	58	-42.553	-52.525	-34.314	-60.684	-23.529
Massive		large	44	20	-54.054	-66.667	-43.182	-75.000	-26.316
Porites		small	14	11	-18.750	-53.333	0.000	-71.429	66.667
	GCB	medium	53	47	-11.290	-30.909	2.222	-43.478	28.571
		large	15	18	22.475	-19.048	58.333	-47.368	133.333

		small	46	16	-65.455	-76.923	-58.537	-83.673	-45.714
	PB	medium	106	67	-36.842	-46.341	-26.966	-52.500	-14.286
		large	23	19	-16.000	-42.857	6.667	-56.000	50.000
		small	22	22	0.000	-33.333	19.048	-52.174	66.667
	SA	medium	40	60	49.468	19.444	74.286	-4.651	118.919
		large	22	17	-21.739	-48.571	-4.000	-65.625	38.462
		small	26	24	-10.620	-41.935	5.263	-55.556	47.619
	EG	medium	127	43	-66.094	-71.875	-60.800	-78.261	-54.310
		large	58	13	-77.442	-84.615	-71.429	-89.655	-62.500
		small	13	0	-100.000	-100.000	-100.000	-100.000	-100.000
	GCB	medium	30	12	-60.000	-75.000	-50.000	-84.848	-29.167
Branching		large	1	1	0.000	-100.000	-65.753	-100.000	44.814
Acropora		small	24	10	-58.333	-75.000	-45.455	-87.500	-22.222
	PB	medium	53	32	-39.173	-50.980	-25.926	-63.158	-11.765
	_	large	17	6	-64.706	-80.000	-50.000	-94.444	-25.000
		small	17	16	-5.719	-38.889	20.000	-65.217	72.727
	SA	medium	52	38	-26.956	-42.857	-12.195	-54.237	8.333
		large	17	17	0.000	-35.294	25.000	-60.000	83.333
		small	5	1	-83.333	-100.000	-75.000	-100.000	-26.419
	EG	medium	15	3	-80.952	-95.000	-72.727	-100.000	-53.846
	_	large	7	1	-87.500	-100.000	-81.818	-100.000	-41.683
		small	0	0	0.000	0.000	0.000	0.000	0.000
	GCB	medium	2	0	-100.000	-100.000	-100.000	-100.000	-82.779
Tabular		large	0	0	0.000	0.000	0.000	0.000	0.000
Acropora		small	5	1	-83.333	-100.000	-71.429	-100.000	-27.202
	PB	medium	8	2	-75.000	-100.000	-66.667	-100.000	-25.000
		large	1	0	-100.000	-100.000	-86.888	-100.000	-77.299
		small	15	11	-27.778	-57.143	-6.250	-73.684	46.154
	SA	medium	68	16	-76.563	-83.636	-71.605	-89.063	-63.636
		large	25	4	-84.615	-93.103	-78.261	-97.297	-63.158



Figure S1: Linear relationship between planar and contour length showing accuracy of conversion of planar length of 4858 coral colonies to their respective 3D contour length using the coral colony rugosity index method (Spearman's rank test: rho = 0.96, t = 206.16, df = 4858, p <0.001).







Figure S2: Non-metric multi-dimensional scaling (nMDS) plots of benthic groups from 16 sites in the Chagos Archipelago, based on Bray-Curtis dissimilarities of square-root transformed

data. Clustering of communities shows variation between depth: shallow (10 m) and moderate (17.5 m) reefs at each atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA).Ellipses represent dispersion of shallow (yellow) and moderate (blue) communities from community centroids at 95% confidence interval. Overlaid benthic groups represent taxonomic groups that significantly contributed to the patterns on the ordination configuration.



Figure S3: Non-metric multi-dimensional scaling (nMDS) plots of hard coral assemblage from 16 sites in the Chagos Archipelago, based on Bray-Curtis dissimilarities of square-root transformed data. Clustering of communities shows variation among atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) across shallow (10 m - white points) and moderate (17.5 m - black points) reefs. Ellipses represent dispersion of each atoll from community centroids at 95% confidence interval. Overlaid coral taxa represent hard corals that significantly contributed to the patterns on the ordination configuration.